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A COMPARISON OF THE PTEROTHORACIC SKELETON AND FLIGHT MUSCLES OF MALE AND FEMALE *LAMARCKIANA* SPECIES (ORTHOPTERA, ACRIDIDAE).

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INTRODUCTION.

THE pterothoracic skeleton and musculature of several ACRIDIDAE have been described previously. The most detailed accounts are those of *Dissosteira carolina* (L.) by Snodgrass (1929) and of *Schistocerca gregaria* (Forskål) by Misra (1947). Maki (1938) has also given a description of the thoracic musculature of the acridids *Locusta migratoria manilensis* (Meyen) and *Atractomorpha ambigua* (Bolivar), but his drawings are very diagrammatic.

A number of ACRIDIDAE have the wings more or less reduced in one or both sexes, and there are many completely apterous species. Modifications in the pterothoracic skeleton and musculature of brachypterous species have been described and discussed by La Greca (1945, 1947), but no similar studies have been carried out on completely apterous species. It appeared of particular interest to study the skeleton and muscles of the pterothorax in a species where one sex is completely apterous while the other has fully developed and functional wings. Such is the case in the pamphagine genus *Lamarckiana*, in all species of which the males have large wings and undertake flights, while the females are completely wingless. Dr. Eric Burtt, at Dr. B. P. Uvarov's request, has kindly collected and fixed in Pampel's fluid specimens of both sexes of *Lamarckiana* sp., on which he published some observations made at Tinde, Tanganyika Territory. In his paper, (Burtt, 1946), photographs of both sexes will be found showing the exceptional degree of wing dimorphism.

The female is larger than the male, and in addition to lack of wings shows various other external differences besides the genitalia. The body is relatively wider, and has a marked hump on the terga of the anterior abdominal segments. The pronotum is a different shape, the ratio of length to height being less than in the male. As only 5 males were available, these and 10 females were measured: the ratio varied between 0·95 and 1·08 in the females with an average of 1·05, and between 1·28 and 1·44 in the males with an average of 1·35.

SKELETON OF THE MALE (figs. 1, 4, 5).

The tergum of the mesothorax is connected by a well-developed intersegmental membrane (fig. 5, *i.m.*) with the prothorax, and by a short one with the metathorax: there is no membrane between the latter and the first abdominal segment. The precosta of the mesothorax (fig. 5, *pc.*) is not clearly visible except in the mid-dorsal region : it is bounded posteriorly by a well-developed antecostal suture, with a corresponding antecosta (*ac.*) on the underside : from the latter, two small phragmata (figs. 4, 5, *1 ph.*) arise, and the antecosta is continued at each side to form a prealar arm (fig. 5, *p.a.*) which

articulates with the first basalare. The rest of the tergum is divided by external sutures and internal ridges into two prescutal regions (*ps.*), a large scutum (*sc.*) and a scutellum (*scl.*). The lateral lobes at the posterior end of the tergum of *Dissosteira* were considered by Snodgrass (1929) to be part of the scutum, but Misra, in consideration of later work of Snodgrass (1935), concludes that they really form part of the scutellum and this view will be adopted here. The posterior end of the scutellum is reduplicated, the fold (fig. 4, *rd.*) extending posteriorly to cover a little of the metatergum (in the figure the mesothorax is shown pulled slightly forward). The lateral margins of the tergum are irregular and thickened : near the front of the scutum are a pair of thin oval patches (fig. 5, *o.p.*).
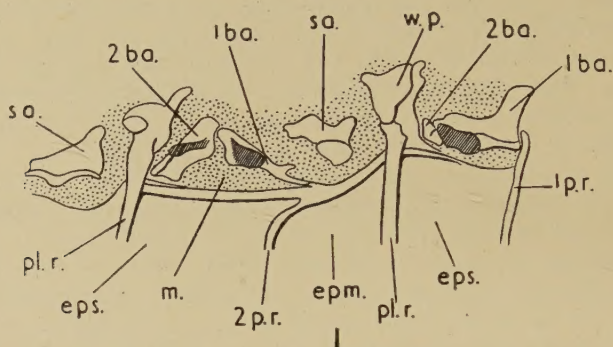
Fig. 1.—Inner view of the epipleurites and the dorsal region of the pleura of the left side of the pterothorax of a male. The shaded areas represent muscle attachments.

The tergum of the metathorax is also divisible into a small precosta (fig. 5, *pc.*), an antecosta (*ac.*) with two phragmata (figs. 4, 5, *2 ph.*), which are, however, well developed, prescutal, scutal and scutellar regions. The scutellum is folded at its posterior end as in the mesothorax. There is a very large postnotum (fig. 4, *pn.*), which represents the sclerotized intersegmental membrane (Misra, 1947). Two very small phragmata (*3 ph.*) which arise from the antecosta of the first abdominal segment are also best described with the metathoracic tergum.

The pleuron of the mesothorax is bounded anteriorly by a more or less vertical ridge (fig. 1, *1 p.r.*), which is continued upwards for a short distance as a dorsal projection. A well-marked ridge (*2 p.r.*) separates it from the metathorax, while the latter is bounded posteriorly for its upper half by a smaller ridge, immediately in front of which is a small thin-walled region. The pleura of meso- and metathorax are each divided into an anterior episternum (*eps.*) and a posterior epimeron (*epm.*) by an internal pleural ridge (*pl.r.*) running approximately parallel with the division between the segments : the pleural ridge expands at its ventral side into a pleural arm. Above each pleural ridge the pleuron is continued dorsally as a wing process (*w.p.*), on to the inner surface of which the pleural ridge extends. There is an internal ridge at the top of the mesothoracic episternum, more marked at its posterior end, a well-developed one at the top of the epimeron and another at or near the top of the metathoracic episternum.

The epipleurites of both pterothoracic segments lie in a membrane between the wing bases and the pleura. In each segment two basalares (*1 ba., 2 ba.*) lie approximately over each episternum and a single subalare (*sa.*) over each epimeron. The mesothoracic epipleurites will be described first : the first basalare is somewhat L-shaped with a short vertical arm ; it bears a well-marked horizontal internal ridge, ending posteriorly in a flattened expansion, facing obliquely upwards and inwards, to which wing muscles are attached. It articulates anteriorly with the dorsal projection at the front end of the episternum and posteriorly with the second basalare. The second basalare is smaller, very roughly rectangular, thickened on its dorsal and ventral edge and bears a well-developed internal ridge : it articulates with the posterior outer face of the first basalare and with the lower end of the wing process. The subalare consists of a shallow cup, with its concave face, to which a wing muscle is attached, ventral, and an irregular piece projecting vertically from the cup. It does not articulate with the pleuron.

In the metathorax the epipleurites are as follows : the first basalare is an elongated epipleurite of irregular shape, with its long axis sloping obliquely backwards and upwards. Towards its posterior end it bears a flattened expansion for the attachment of wing muscles, and has a marked upward and inward projection about half-way between this and the anterior end. The second basalare is also elongated and forms an oblique angle with the first : along its long axis it bears posteriorly an internal ridge, which joins the more anterior flattened projection to which wing muscles are attached. Anteriorly it articulates with the first basalare and posteriorly with the top of the episternum just in front of the wing process. As in the mesothorax, the subalare is formed of a shallow cup with the concave side ventral, and a rather triangular vertical piece.

Details of the ventral side of the pleura and of the sterna will not be given, as they have no direct bearing on this study.

Skeleton of Female Compared with that of Male (fig. 2).

If the pterothoracic skeleton of a female *Lamarckiana* sp. is compared with that of a male a number of differences are seen. It is more heavily sclerotized and the terga are immovably joined to the pleura, no free epipleurites or membranes being present between them : the intersegmental membrane between the meso- and metathoracic terga is also lacking.

The pterothoracic terga do not show clear division into as many regions as in the male. In the mesothorax there is a precosta (*pc.*) that narrows or disappears in the mid-line, a well-marked antecostal suture with a corresponding internal antecosta (*ac.*), which, however, bears no phragmata, but the rest of the tergum is not obviously divided into prescutum, scutum and scutellum. There are certain sutures, corresponding with the internal ridges shown in fig. 2, but the significance of these latter will be considered after the musculature has been described. The posterior end of the tergum is folded on itself (*rd.*) in its middle region, but this folding does not extend to the edges, and the upper and lower sides of the fold are partly fused. Two thin oval patches (*o.p.*) are present at the front end as in the male.

In the metathorax a small anterior part in the region of the mid-line underlies the posterior part of the mesothoracic tergum, and this appears to be the

precosta. There is a well-developed antecosta (*ac.*), with its corresponding external antecostal suture, and, as in the mesothorax, it bears no phragmata. There is again no clear division into prescutal, scutal and scutellar areas, but certain sutures with underlying ridges are present. The central region of the posterior part of the tergum is folded, but there is no large postnotum as in the male.

The pleural ridge (*pl.r.*) of the metathorax runs more obliquely than in the male, in such a way that the episternum (*eps.*) of this segment becomes very narrow at its dorsal end. The reduction in size of the wing muscles which lie between the pleural ridge and the front of the episternum may make this
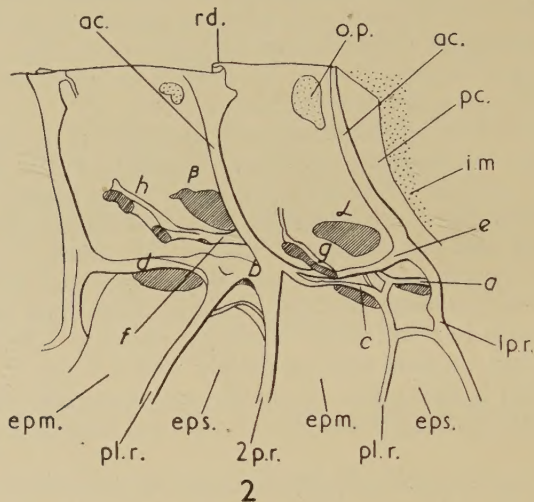
Fig. 2.—Inner view of the terga and the dorsal region of the pleura of the left side of the pterothorax of a female. The shaded areas represent muscle attachments.

possible, and it may be that the presence of a more or less diagonal ridge provides greater strengthening for the pleuron than would a ridge running parallel with its sides. The position of the well-developed ridges to be found in the region of the junction of the terga with the pleura can be seen from fig. 2.

The absence of membranes in the female between the mesothorax and metathorax and between the pterothoracic terga and pleura may be correlated with the absence of wings. As Snodgrass (1929) points out, " the wing mechanism demands at least a limited freedom of movement in the wing-bearing terga," but as the female is completely apterous there is presumably no need for such movement. It may indeed be advantageous to have that section of the body to which the third legs, the chief locomotor organs, are attached, in the form of a rigid cylinder.

Flight Muscles of the Male (figs. 3, 4, 5).

A description of the flight muscles and those which may be associated with flight in the male will be given first, and then those of the female will be compared with them. The main muscles fall into the two groups characteristic

of pterygote insects—direct and indirect. Both of these groups in *Lamarckiana* sp. are similar to those described by Snodgrass (1929) for *Dissosteira* and by Misra (1947) for *Schistocerca gregaria*, but *Lamarckiana* contains some small muscles not present in either of these species, and which may aid the indirect flight muscles.

The chief indirect muscles are the dorsal longitudinal muscles, which on contraction will increase the curvature of the tergum and cause the lowering of the wings, and the tergo-sternal muscles, which by contraction will decrease the curvature of the tergum and thereby raise the wings.

The following muscles, with the exception of the dorsal transverse muscle, are paired in *Lamarckiana* sp. :
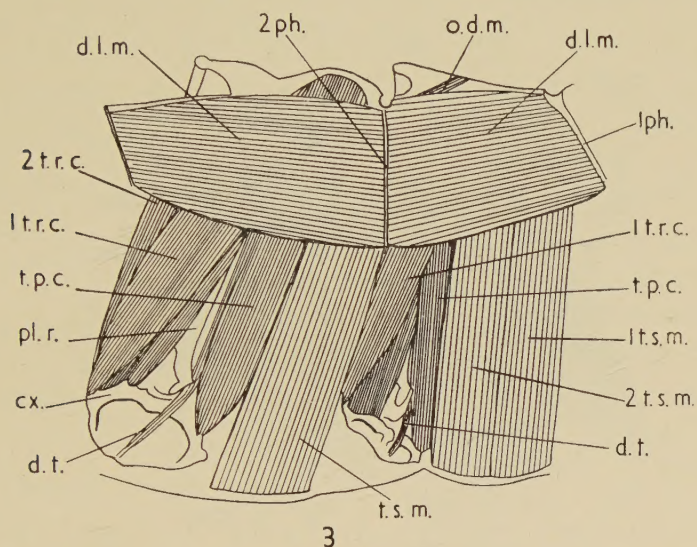
FIG. 3.—Inner view of the muscles of the left side of the pterothorax of a male : the ventral longitudinal muscles and some of the leg muscles have been removed.

The *dorsal longitudinal muscles* (fig. 3, *d.l.m.*) are very large in both meso- and metathorax. In the former the muscle passes from its anterior attachment on the first phragma and antecosta to the anterior face of the second phragma. In the metathorax it is a longer muscle, attached anteriorly to the posterior face of the second phragma, and posteriorly partly to the postnotum and partly to the third phragma and antecosta.

There are two *oblique dorsal muscles* in the mesothorax, a longer dorsal one and a shorter ventral one (figs. 4, 5, *o.d.m.*). They both arise on the precosta of the metathorax, the dorsal one being attached by a broad tendon-like structure. The dorsal one passes obliquely upwards and forwards, and is inserted at the junction of the scutum and the median lobe of the scutellum : the more ventral one passes obliquely forwards, upwards and outwards to its insertion on the posterior face of the ridge separating the scutum from the lateral lobe of the scutellum. These muscles are similar to those described by Misra (1947) for *Schistocerca gregaria*, and the dorsal one, according to Misra, corresponds to the single one present in *Dissosteira* (Snodgrass, 1929). They

also appear to correspond to the lateral dorsal muscles described by Maki (1938) for *Locusta*. Oblique dorsal muscles are not generally present in the metathorax, but in one individual very small ones were found. Snodgrass (1935) suggests that these muscles supplement the tergo-sternals; Misra (1947) also states that the two oblique dorsal muscles in *Schistocerca* help the tergo-sternal muscles in depressing the scutellum, but it seems more likely in *Lamarckiana* sp. that they would increase the curvature of the scutellum.

The *dorsal transverse muscle* (fig. 5, *d.t.m.*) is a small unpaired muscle passing transversely across the median lobe of the scutellum, and attached to it at either side; it passes above the more dorsal of the oblique dorsal muscles. This muscle is found in the mesothorax, but is not always present in the meta-
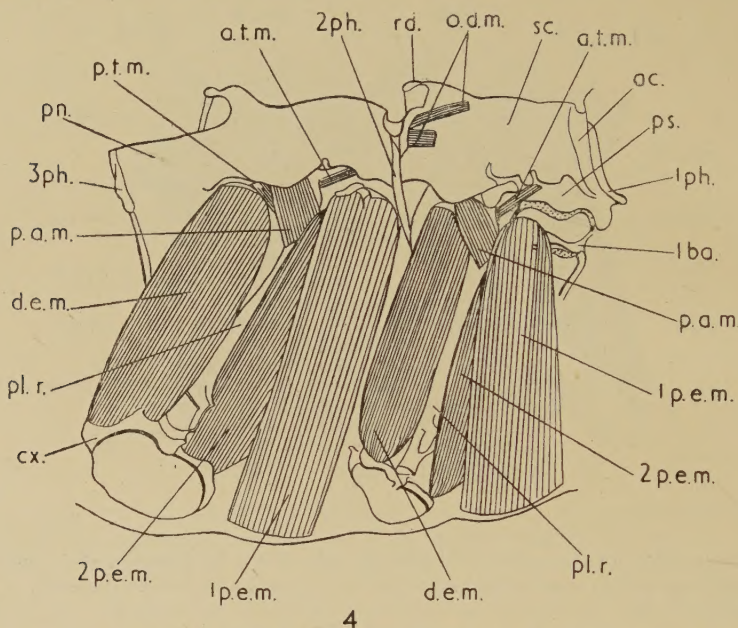
Fig. 4.—Inner view of some of the flight muscles of the left side of a male : the dorsal longitudinal and the tergo-sternal muscles have been removed.

thorax. Its function appears to be to increase the curvature of the middle lobe of the scutellum, and at the same time either decrease the curvature of the lateral lobe of the scutellum, or if this remains constant, to pull the posterior part of the lateral edge of the tergum slightly nearer the mid-line. No similar muscle appears to have been described previously in ACRIDIDAE.

The large *tergo-sternal muscles* (fig. 3, *t.s.m.*) are situated in the front part of each of the pterothoracic segments. Two muscles are present in the meso-thorax, both of which arise from the sternum in front of the second leg and pass outside the dorsal longitudinal muscles. The first (*1 t.s.m.*) or most anterior is inserted mostly on the prescutum, but has one branch going to the scutum ; the second (*2 t.s.m.*) has most of its fibres inserted on the scutum, but some just behind those of the first on the prescutum.

The single tergo-sternal muscle (*t.s.m.*) of the metathorax arises on the

sternum in front of the third leg, and runs upwards and slightly forwards to its insertion on the metathoracic antecosta and prescutum and sometimes on the second phragma.

Tergo-pleural muscles are present, but their degree of development varies in different individuals : all however are small.

The *anterior tergo-pleural muscle* (figs. 4, 5, *a.t.m.*) arises from the anterior side of the pleural ridge (sometimes where this has passed into the wing process). In the mesothorax it runs anteriorly and obliquely upwards and inwards to its attachment near the posterior end of the prescutum, passing outside the second tergo-sternal muscle : in the metathorax it passes to a small sclerite near the junction of scutum and prescutum.
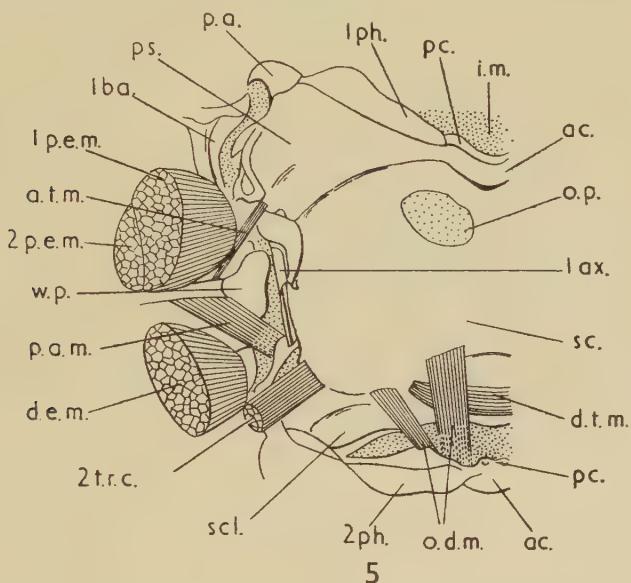
Fig. 5.—Inner view of the dorsal region of the right half of the meso- and part of the metathorax of a male : the tergum is shown somewhat flattened. The dotted areas represent membrane and the broken lines tendon-like muscle attachments.

The *posterior tergo-pleural muscle* (fig. 4, *p.t.m.*) arises from the posterior side of the pleural ridge, sometimes partly overlapping the pleuro-alar muscle (see below) externally, and passes obliquely backwards to its insertion on, or sometimes near, the edge of the tergum close to the junction of the scutum and the lateral lobe of the scutellum. This muscle is usually only found in the metathorax, but one individual was examined in which it was also present in the mesothorax.

This last specimen showed other additional muscles (not figured). A muscle arising from the ridge at the front end of the mesepisternum passed obliquely backwards to its insertion on the mesothoracic tergum near the junction of scutum and prescutum, and another from the ridge between the two pterothoracic pleura passed back to a similar insertion in the metathorax. There was also a very small muscle passing obliquely forward from the anterior

side of the second phragma to the lateral lobe of the scutellum and a corresponding one in the metathorax.

No tergo-pleural muscles were described by Snodgrass (1929) for *Dissosteira*, but Misra (1947) found a stout muscle (the tergo-pleural dorsal muscle) in the mesothorax only of *Schistocerca* ; this is probably homologous with the small anterior tergo-pleural muscle of *Lamarckiana*. Maki (1938) described three tergo-pleural muscles in *Locusta*, of which two are probably homologous with the anterior and posterior ones of *Lamarckiana*. Misra considers that the tergo-pleural dorsal muscle in *Schistocerca* arches the prescutum, and through an accessory sclerite helps the down-stroke of the wing. From its insertion the similar one in *Lamarckiana* does not appear to have this effect, but rather to depress the posterior part of the prescutum. The other tergo-pleural muscles seem unlikely to have any important function, as they are not constant in their appearance.

The direct wing muscles are the pronator-extensors, the depressor-extensors and the flexors.

The *first pronator-extensor muscle* (fig. 4, *1 p.e.m.*) is attached ventrally to the sternum, just outside the tergo-sternal muscle or muscles, in both pterothoracic segments. In the mesothorax it is inserted entirely on the flattened ledge of the first basalare ; in the metathorax it is inserted partly on the ledge of the first basalare and partly on the ledge of the second.

The *second pronator-extensor muscle* (*2 p.e.m.*) is attached to the anterior and outer side of the coxa of the leg. It is attached dorsally to the ledge of the first basalare in the mesothorax ; in the metathorax most of its fibres are inserted on the ledge of the second basalare, but a small branch passes to that of the first basalare. In *Dissosteira* (Snodgrass, 1929) and *Schistocerca* (Misra, 1947) the second pronator-extensor is attached to the second basalare only, in the metathorax.

The *depressor-extensor muscle* (*d.e.m.*) in the mesothorax passes from its ventral attachment on the posterior and outer side of the coxa to the concave ventral side of the subalare. That of the metathorax has similar attachments, but is better developed than in the mesothorax.

The *pleuro-alar muscle* (*p.a.m.*) in both segments arises from the pleural ridge and passes obliquely backwards and upwards to the base of the wing, where it is inserted on the third axilla.

Snodgrass (1929) concludes that the direct muscles in *Dissosteira* have the following effects : the pronator-extensors deflect the anterior margin of the wing, and the depressor-extensor deflects the posterior part, and also depresses the wing : the pleuro-alar folds the wing, and the pronator-extensors and the depressor-extensor probably extend it. Misra (1947) prefers to call the muscles that deflect the costal margin of the wing " rotators " rather than " pronators," since he does not consider the movement the same as that of pronation in a vertebrate limb.

FLIGHT MUSCLES OF FEMALE (fig. 6) COMPARED WITH THOSE OF MALE.

The flight muscles of the female show a number of differences when compared with those of the male.

The chief indirect muscles, that is, the dorsal longitudinal and the tergo-sternal muscles, are very much reduced in both pterothoracic segments : this

might be expected since their chief, or only, function is to bring about movement of the wings.

The *dorsal longitudinal muscles* are represented only by strands of fibres (not figured). The extent to which they are developed seems to vary somewhat in different individuals, but they never appear strong enough to cause any alteration in the curvature of the tergum.

The *oblique dorsal muscles* differ little in size from those of the male.

The *dorsal transverse muscle* is entirely absent in both pterothoracic segments.
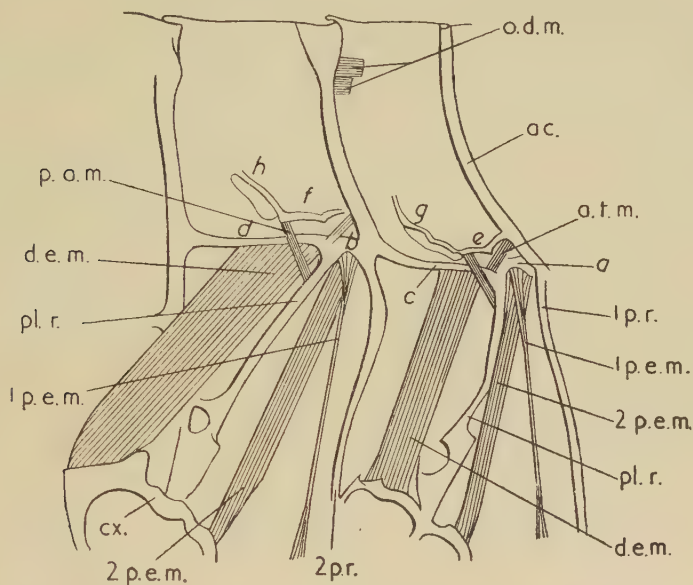
FIG. 6.—Inner view of some of the flight muscles of the left side of a female : the dorsal longitudinal and the tergo-sternal muscles have been removed.

The *tergo-sternal muscles* (not figured) in both meso- and metathorax are represented only by strands, the fibres of which tend to diverge at their ventral ends ; like the dorsal longitudinal muscles they do not look as if they could alter the shape of the tergum.

The *anterior tergo-pleural muscle* (*a.t.m.*) of each segment does not appear to be much smaller than in the male : it arises from near the top of the pleural ridge (though there is no wing process) and passes to the tergum. A small muscle (*p.a.m.*), passing dorsally and posteriorly from the posterior side of the pleural ridge to the tergum, may be either the posterior tergo-pleural or the pleuro-alar muscle, but as it is usually present in meso- as well as metathorax, it is more probably the pleuro-alar, with which in the metathorax the posterior tergo-pleural may have become incorporated.

The direct wing muscles show varying degrees of reduction when compared with those of the male, and there is some variation in different specimens.

The *first pronator-extensor muscle* (*1 p.e.m.*) of both meso- and metathorax

is represented only by a few strands, in which however cross-striations have been seen in one or two specimens : these strands tend to fan out at their dorsal and ventral attachments.   It arises from the sternum in meso- and metathorax, and in the former passes to its insertion below ridge a, which joins the pleural ridge with the ridge in front of the episternum, and in the latter to the junction b, of the corresponding ridges.

The *second pronator-extensor muscles* (*2 p.e.m.*) are quite well developed, but relatively smaller than in the male.   Each arises as in the latter from the anterior outer side of the coxa, and passes to its dorsal insertion with the first pronator-extensor.

The *depressor-extensor muscle* (*d.e.m.*) of each segment is also fairly well developed and arises from the posterior and outer side of the coxa ; in the mesothorax it passes to ridge c and in the metathorax to ridge d instead of to a basalare as in the male.   The significance of these and other ridges will be discussed later.

The muscles which appear to represent the *pleuro-alar* muscles (*p.a.m.*) are inserted on the posterior side of the pleural ridge in each pterothoracic segment.   In the mesothorax the muscle passes obliquely posteriorly and dorsally to its insertion below the internal ridge e, near the junction of this with the elongated projection g, and in the metathorax it passes in a similar direction to the union of ridge f with the projection h.   As already noted, these muscles may possibly represent the posterior tergo-pleural muscles as well.

According to Snodgrass (1929) the first pronator-extensors may be muscles specially developed for the wings, while the second pronator-extensors and the depressor-extensors are essentially leg muscles, which, however, are used as wing muscles in the adult.   This may help to explain why the first-named muscles are much reduced in the female *Lamarckiana* sp., while the last two are relatively well developed.   It is probable that with the absence of movable epipleurites and flexible membranes between pleuron and tergum, the second pronator-extensor and the depressor-extensor of each segment can work together as abductors of the coxa, as they do in nymphal Orthoptera.

<center>DISCUSSION.</center>

The lack of free epipleurites in the female *Lamarckiana* should presumably be considered an extreme form of the micropterism found in some other PAMPHAGINAE, e.g., *Pamphagus marmoratus* Burm., where there is no membranous region between the epipleurites and the pleura (La Greca, 1945).

By comparing some of the muscle insertions in the male and female it is possible to suggest homologies between parts of the two exoskeletons in the tergo-pleural region, but certain difficulties are encountered.

In the mesothorax of the female the pronator-extensor muscles are attached dorsally beneath ridge a and the depressor-extensor muscle below ridge c, so that ridge a should represent the ledge of the first basalare, and all or part of ridge c the lower part of the subalare, of the male.   In the mesothorax of the male a small branch of the tergal promotor of the coxa, which is connected ventrally with the rest of the muscle by a long tendon, is attached dorsally to the ridge between the scutum and prescutum, and a branch of the depressor of the trochanter (fig. 3, *d.t.*) is attached nearby to the edge of the scutum. In the female these muscles are inserted on ridge e, suggesting that the anterior

part of the ridge represents the ridge between scutum and prescutum and the posterior part represents part of the edge of the scutum.

If these suggestions are correct, then that part of the skeleton between ridge *e* and ridges *a* and *c* must represent the prescutum, part of the first basalare and subalare, the second basalare and perhaps some sclerotized membrane ; the part above ridge *e* will all be scutum. This view is supported by the fact that another branch of the tergal promotor muscle and another branch of the depressor of the trochanter, as well as the first tergal remotor of the coxa, all of which are attached to the scutum in the male, arise from region α (fig. 2) above ridge *e* in the female.

The pleuro-alar muscle of the mesothorax is inserted dorsally near the posterior end of ridge *e*, and since it is attached to an axillary sclerite in the male, its attachment to a ridge representing the edge of the tergum in the female seems probable.

The second tergal remotor of the coxa in the male is inserted chiefly on the inner side of the ventral edge of the scutum, but a very small part of it extends on to the ridge separating scutum from scutellum : in the female it is inserted on the posterior face of ridge *g*. It seems possible then that most of this ridge, together with a small dorsal projection to which the anterior end of the ventral part of the oblique dorsal muscle is attached, may represent the ridge which in the male separates the scutum from the lateral lobe of the scutellum : if this is so, then at any rate most of the region behind *g* would be part of the scutellum.

Similar comparisons can be made between the muscle attachments in the metathorax of male and female. In the male, however, the second tergal remotor of the coxa arises on the lateral part of the scutellum itself, although in the female it is attached to the posterior face of ridge *h* ; if this latter ridge represents the ridge between the scutum and the lateral part of the scutellum, the muscle insertion must have become shifted rather forward.

It can be seen from the above that many parts of the pterothoracic exoskeleton of the male can probably be traced in the female, although the latter has become very much modified in correlation with its apterous condition.

SUMMARY.

1. The male has well-developed wings ; the female is completely apterous.

2. The exoskeleton of the male is less heavily sclerotized than that of the female.

3. The tergum of meso- and metathorax is more convex in the female than in the male.

4. The male has free epipleurites, but these are not present in the female.

5. An intersegmental membrane is present between the meso- and metathoracic terga in the male, but not in the female.

6. The prescutal, scutal and scutellar areas of the terga are well defined in the male, but not so obvious in the female.

7. The male has three pairs of phragmata, but these are absent in the female.

8. There is a large postnotum in the metathorax of the male, but not in the female.

9. The pleural ridge of the metathorax runs parallel with the long sides of the latter in the male, but somewhat diagonally to them in the female.

10. The dorsal longitudinal muscles and the tergo-sternal muscles are well developed in the male, but only represented by strands in the female.

11. The dorsal transverse muscle found in the mesothorax and sometimes in the metathorax of the male is absent from the female.

12. The first pronator-extensor muscles are well developed in the male but only represented by strands in the female.

13. The second pronator-extensor muscles are relatively considerably smaller, and the depressor-extensor muscles somewhat smaller in the female than in the male.

14. The pleuro-alar muscles are less well developed in the female than in the male.

15. The posterior tergo-pleural muscles are either absent or fused with the pleuro-alar muscles in the female.

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Abbreviations used in the Figures.

ac., antecosta. *a.t.m.*, anterior tergo-pleural muscle. *1 ax.*, 1st axillary sclerite. *1 ba.*, *2 ba.*, 1st, 2nd basalare. *cx.*, coxa. *d.e.m.*, depressor-extensor muscle. *d.l.m.*, dorsal longitudinal muscle. *d.t.*, branch of depressor of trochanter. *d.t.m.*, dorsal transverse muscle. *epm.*, epimeron. *eps.*, episternum. *i.m.*, intersegmental membrane. *m.*, membrane. *o.d.m.*, oblique dorsal muscle. *o.p.*, oval patch in tergum. *p.a.*, prealar arm. *p.a.m.*, pleuro-alar muscle. *pc.*, precosta. *1 p.e.m.*, *2 p.e.m.*, 1st, 2nd pronator-extensor muscle. *1 ph.*, *2 ph.*, *3 ph.*, 1st, 2nd, 3rd phragma. *pl.r.*, pleural ridge. *pn.*, postnotum. *1 p.r.*, ridge at front of mesopleuron. *2 p.r.*, ridge between meso- and metapleuron. *ps.*, prescutum. *p.t.m.*, posterior tergo-pleural muscle. *rd.*, reduplication of tergum. *sa.*, subalare. *sc.*, scutum. *scl.*, scutellum. *t.p.c.*, tergal promotor of coxa. *1 t.r.c.*, *2 t.r.c.*, 1st, 2nd tergal remotor of coxa. *1 t.s.m.*, *2 t.s.m.*, 1st, 2nd tergo-sternal muscle. *w.p.*, wing process. *a, b, c, d, e, f, g, h*, indicate ridges referred to in text. α, muscle attachment referred to in text. β, corresponding muscle attachment in metathorax:

ON THE BEHAVIOUR OF NIGHT-FLYING INSECTS IN THE NEIGHBOURHOOD OF A BRIGHT SOURCE OF LIGHT.

By H. S. Robinson.

1. Congregation to Light.

The experiments by my brother and myself into the reactions of night-flying insects in the field of bright lights have not established any new or startling facts. What they have done is to enable us to bring together a number of critical observations of behaviour, and to weave from them a workable hypothesis to explain what happens when a lamp is placed in an area where insects are flying. It should, I think, be explained that our experiments have been piecemeal and *ad hoc* and have, of necessity, been of a comparatively crude nature. It is my hope that they will be critically tested by others with proper facilities for control. Our work has been principally concerned with night-flying Lepidoptera, but the general conclusions seem to be fairly applicable to other orders. More, however, will be said on this point when flight inhibition is dealt with.

In order that the reasons for the experiments performed and the conclusions made can be appreciated it will probably be best to relate the various stages of intention and thought which we followed. Our original intention was very simple. It was to construct, on classical lines, a unidirectional light-trap to obtain local species in order to establish a small collection. Our discussions, our reading, and our observation of similar traps led us to assume, quite uncritically, that night-flying insects were attracted to lights, the attraction being in the nature of that exerted by a female moth in assembling the males. From published notes and observations it seemed that there was some sexual significance in the so-called attraction of light and it is frequently stated that, as regards certain species, only one sex comes to light.

With this information we constructed a small trap on the slotted-glass principle and used in it lamps of various types. We also did some experiments on altering the angles of the glass screens, painting the inside, and finally constructed traps of various sizes. All this work was, of course, based on the assumption that insects outside such a trap would use their best endeavours to reach the lamp, and would, therefore, go inside as long as the light was on.

Even at this early stage, however, we met some puzzling examples of particular species which, while congregating in the vicinity of the trap, seemed reluctant to enter it. We also observed that when very small light-sources of low voltage and high power were used more species seemed to enter the trap than when larger, more diffuse lamps were used. We soon realized, however, that no critical experiments were possible with this type of trap. Being operative in one direction only, accidents of locality, wind, background, etc., made catches so variable that no useful purpose was served by counts.

At this point we heard of the extremely ingenious trap designed and used at Rothamsted. This trap is, of course, not directional, though it does still operate on the attraction principle. We constructed two traps of this design

and renewed our efforts to discover the best method of using them. The use of two traps enabled us to perform a series of crude controlled experiments on various types of lamp and our results are reported in the *Entomologist's Gazette* (1950, **1** : 3–20).

In general we found, again, that the trap was most effective with a small bright light-source. We concluded from our observations that the higher the surface brilliance of a lamp, the smaller was the area in which insects congregate. Increases of power, however, made the area of congregation larger. Thus, species which failed to enter the trap with certain lamps would appear in the trap if the surface brilliance was increased, even though no power increase was made. On the other hand, however great a power increase was made, as long as the surface brilliance was unaltered, species remained obstinately outside. It was this fact which was our greatest puzzle—if insects were attracted to lights, why should they fail to get to them when they approached within a comparatively short distance, and why was this inability apparently a property of particular species ?

There was, of course, no doubt that the insects were congregating in the neighbourhood of the lamp, but we could find, in published literature, nothing which would suggest any reason why, if they were not attracted by the light, they should do this. The only approach we could make was an anthropomorphic one, and it occurred to me that there was a comparable human reaction. If one comes within view of a bright light against a background of total darkness, there is a tendency to turn towards it. This tendency is very readily observable when driving a car towards a bright light, e.g., the headlight of another car. There is an involuntary tendency, against which considerable reason must be used, to swerve into the light.

We have, subsequently, had our attention drawn to the unilateral muscular contraction in insects described by Loeb, and the two reactions appear to be allied. This phenomenon we have referred to as " dazzle," but there is no reason why this term should be retained if it is misleading. Perhaps " unbalance " would be better. A consideration of this aspect revealed a much more manageable hypothesis to explain the behaviour of insects and, after prolonged study of the paths of flight, we became convinced that this hypothesis was somewhere near the truth. Few insects actually came to a free light ; all circled it at greater or less distance and these distances were, in general, different for different species.

The hypothesis explained, too, the greater effectiveness of high-brilliance lamps, as the phenomenon of dazzle depends, not on the power of the light seen but on its surface brightness as compared with the background. We found that, in general, insects with heavy bodies and small wings which flew fast circled the lamp very closely, whereas those with larger wings, smaller body, and slower flight, congregated further out. We decided, accordingly, to test the hypothesis by endeavouring to construct a trap which depended in no way on attraction, but operated solely on the unbalance effect of dazzle. At the same time we made some experiments to secure a lamp of very high surface brilliance for a given power. Fig. 1 indicates the construction finally adopted.

The trap proper is, basically, the upper structure consisting of an inverted truncated cone containing a number of radial vanes with, at the centre, a small light source lying just above the plane through the top of the cone.

In theory such a construction produces a hemisphere of illumination with centre at the centre of the cone, and basal plane coincident with the plane through the top of the cone. An insect within the hemisphere performing a planar transit of the lamp must, therefore, be above the hemisphere base when
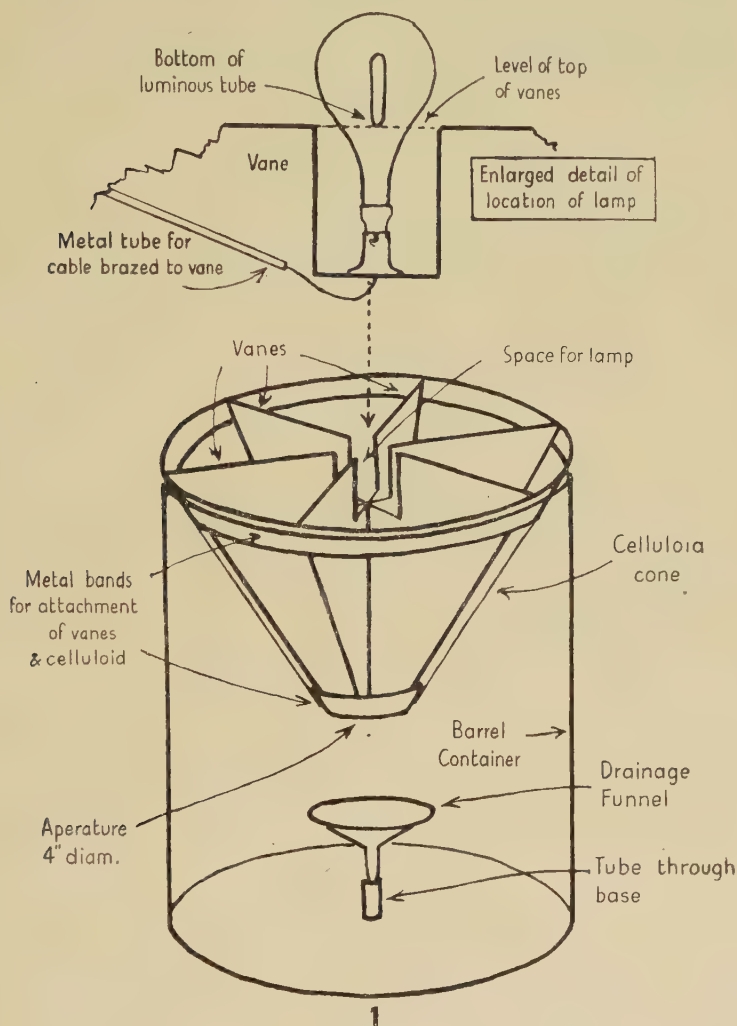
FIG. 1.—Light trap with 2-foot diameter mouth.

it starts and must pass through this plane on the far side of the lamp. If the transit is within the cone aperture the insect will, as soon as it passes below the top, strike one of the vanes. This reduces its flying speed, causing it to stall and fall into the cone and thence into a suitable receptacle beneath.

The receptacle we use is a barrel or box in which tetrachlorethane is evaporated electrically at a sufficient vapour concentration to anaesthetize but not to kill. In order to prevent the escape of insects the cone is mainly

constructed of transparent material so that the point of exit may be invisible from the interior.

As will be seen, the trap is a compromise between the requirements of theory and the limitations of practice. In theory the cone mouth should be infinitely large or the light source infinitely small, otherwise the basal plane is not a plane but a shallow cone, and upwards transits, which are ineffective, are possible. There is, as will be seen later, a further and graver objection to this cone of light. Our original trap was two feet in diameter—but only because we were
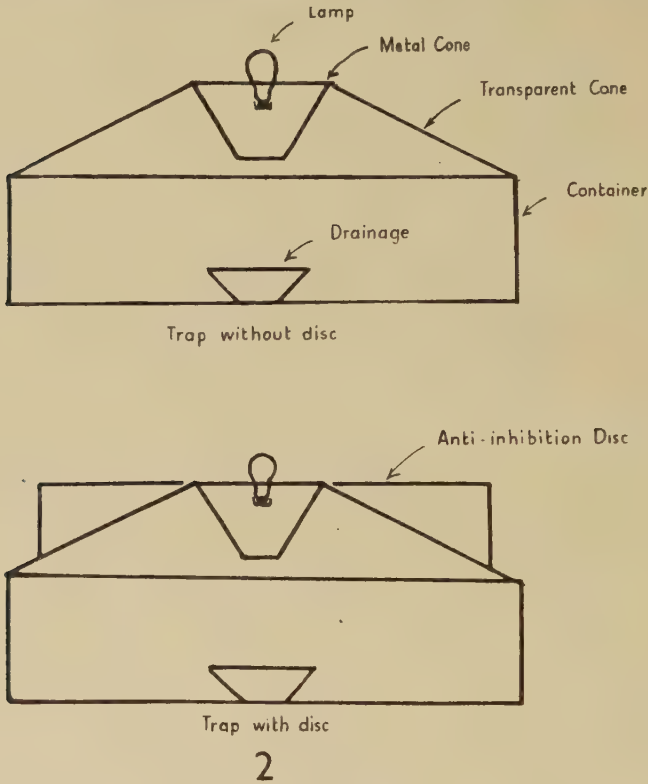
FIG. 2.—Simplified sectional diagram of portable trap.

able to obtain conveniently a barrel of this size. This somewhat unwieldy construction has been adapted by my brother, who has produced a compara- tively light and portable trap, of which a sketch appears at fig. 2.[1]

In designing the trap we considered the most effective source of light to use in it. It will be recalled that we had established, fairly conclusively, that increasing the power of a lamp increased, as might have been expected, the area over which it operated and therefore the number of insects congregated about

[1] This latter design, while not quite as effective for sampling as the static trap shown in Fig. 1, is useful where portability is essential (as in collecting insects in various localities), and has been registered by Mr. P. J. M. Robinson as Design No. 862769 and commercially produced. There is no such restriction on the construction or use of the static trap.

it, but the area of congregation was proportionately increased. If, however, surface brilliance was increased the area of congregation was lessened. Put in another way, what we found was that as power was increased more insects were collected in the trap, whereas when surface brilliance was increased more species were taken. Clearly, therefore, if our hypothesis were correct, an increase of power and surface brilliance should produce an increase in both insects and species.

There was here a further factor to be considered, namely the colour or spectral content of the light used. There was no reason to suppose that a lamp which appeared bright to the human eye would of necessity appear bright to the insect eye, and it was, accordingly, necessary to take into account the range of insect vision.

Eltringham quotes Imms as giving this range for bees in daylight as 3000° A to 6500° A, i.e., from a point in the ultra-violet to a point in the orange red. Our experiments led us to believe that the upper limit given is a little high for night-flying moths. Moths appear to be almost wholly insensitive to sodium light, which is fairly monochromatic at 5900° A, but sensitive to all colours of shorter wavelength. We agree that the lower limit is about 3000° A. It may be fairly assumed that the sensitivity curve is continuous and fairly symmetrical between these ranges (as in the mammalian eye) until the contrary is proved.

If this assumption is made, the peak of insect sensitivity should lie at about 4500° A, that is to say at the limit of human vision in the violet. This means that, for a given power, a light of the maximum apparent brightness for an insect will be of almost the minimum apparent brightness to the human eye. Thus, for a lamp to be effective for operation in a trap, high output is necessary in the ultra-violet and blue regions of the spectrum, the remaining output in the visible spectrum being of little value. A lamp giving such an output is not commercially available and the output of a filament lamp, even at very high temperatures and consequently of short life, is mainly in the long-wave region of visible light. The mercury vapour lamp, however, has a comparatively large output in the insect range and the human range, and is very suitable. In the high-pressure mercury lamp, too, it is possible to obtain a small source and high brilliance. It was accordingly decided to use a lamp of this type in the trap.

The preliminary experiments with the trap and mercury vapour lamp were very satisfactory and very large numbers of insects of many species were taken. As some guide to the possibilities it may be noted that, in late August, 1949, one of these traps took, at Alton in Hampshire, over 25,000 insects on each of three successive nights. A controlled test of one of the traps by Dr. Williams of Rothamsted indicated that they are substantially better than anything previously designed. As a matter of interest, Dr. Williams considers that the improvement is due in equal parts to the efficiency of the lamp and the design of the trap.

It will thus be seen that the hypothesis of dazzle has resulted in the construction of an effective design. If, however, the hypothesis is accepted as a whole, it leads to a significant departure from old ideas. For instance, if we consider that insects are attracted, it should be possible with a powerful lamp in an elevated position to draw to the light a vast assembly of insects from

surrounding areas. If, on the other hand, assembly depends on the chance entry of insects in normal flight into the field and their consequent diversion by dazzle, no such result will occur. The insects congregated will be only those which normally fly in the particular ecological area occupied by the field of the lamp, and insects will not be, as it were, sucked out of another area into one which they do not normally occupy. In other words, if the principle involved is one of attraction, movements of the lamp over small distances will make little difference to the size or content of the catch. If the principle is dazzle, the size and content of the catch will be governed solely by locality.

We find, in fact, that using 80–150 watt lamps, movements of the trap over as little as fifty yards may produce catches substantially different both as regards numbers and species even where the alternative sites are clearly visible one from the other. It seems quite clear that insects further than this distance from the light source are almost unaffected by it. I shall discuss later whether they may be repelled from the lighted area.

The traps may, therefore, be confidently used to take precise and discrete samples of night-flying insects in a small area—but it should be remembered that the area *is* small and, if it is desired to take a district sample, traps should be laid at intervals of not less than 100 yards where there is obvious ecological variation.

In this connection it is interesting to consider the old opinion that the attraction to light is of a sexual nature and mainly affects male insects. As far as we are able to discover, the sexes, if they are night-flying, are equally susceptible to diversion to bright lights and any differentiation, in representative catches, is due to the fact that the two sexes fly in different areas. It is possible, e.g., in the case of *Trichiura crataegi* (L.)—the pale eggar moth—to obtain, by suitable choice of locality, either sex at will.

It should be noted that the dazzle reaction appears to be a phenomenon wholly apart from normal perceptive vision, the extent of its effect increasing as facilities for perception are withdrawn and decreasing as perception is brought into play. Thus, if a trap be tested in a position where the light illumines some nearby object, e.g., a bush, the congregation of insects is considerably less than when no such object is present. For this reason the matter of background is of some importance and, where trapping is used for pest control, the trap sites should be so chosen as to be well clear of illuminated objects.

2. Inhibition by Light.

The next matter of interest in connection with insect behaviour involves a degree of physiological speculation, and, though the behaviour to be described is readily observable, it might well form the subject of detailed research. It has been stated that night-flying insects are inhibited from flying by exposure to some degree of general lighting. The degree of illumination required appears to be about that of bright moonlight, and a number of observers have confirmed that general flight is considerably reduced on moonlight nights.

The nature of the mechanism in the compound eucone eyes of moths which causes them to be adapted for various light levels has been frequently described.

The detailed operation of this mechanism is, to some extent, still obscure, but it is clear that, basically, the process is similar in effect to that of the iris in the mammalian eye.

When the insect eye is in the sensitive condition, with the dye area drawn away from the cone base, the eye of the insect appears to glow by light reflected from the interior. When the eye is in the insensitive condition with the dye area covering the whole cone, the eye appears quite dark.

A very striking experiment can be performed which leads to an interesting speculation regarding this sensitizing mechanism.

If several hundred lightly anaesthetized moths are spread on a flat surface (a condition which occurs sometimes in our traps) and there is placed on the layer a piece of opaque material cut into any convenient pattern, and the whole is left for an hour or two exposed to light, the insects outside the pattern have their eyes desensitized while those below the pattern become sensitized. At the same time the effect of the anaesthetic wears off. If, now, the pattern is removed it will appear in the layer of moths in reproduction as a pattern of glittering points where the sensitized eyes glow. If the conditions have been correctly arranged the sensitized insects will be quite lively, and will crawl, fly and climb over and under the desensitized insects preferably into a dark place. The insensitive insects outside the pattern, however, remain quiescent and, in a short time, there will be a clear space where the pattern has rested.

This type of behaviour leads us to think that desensitization of the eye causes, or is closely connected with, flight inhibition. Whatever its cause, flight inhibition can be shown to be a substantial factor in the pattern of behaviour. If this were not so, it should be possible to congregate insects most readily to a lamp which gives light in all directions, and any cutting off of the light, in any direction, should reduce the number of insects taken. A test is quite simple. It is possible to construct two traps, their only difference being that one has a disc below the lamp which prevents light falling on the ground, whereas the other has not. It will be found that the catch of the trap with the disc is always substantially greater than that without it (fig. 2).

It is suggested that the reason for this can only be that inhibited insects which settle around the trap will, if the light continues to reach them, remain inhibited. If, however, on settling they are in the dark below the shadow edge of the disc they will be resensitized and commence to fly. As soon as they do so they rise again into the dazzle area and are brought nearer to, and finally into, the trap. It would not appear that the phenomenon of inhibition occurs in all orders. Some of the midges and gnats seem to fly indefinitely in bright light, and the same thing seems to obtain in some beetles. It may be that the eye construction is the governing factor, but this is not a matter into which we are qualified to research.

3. Repulsion by Light.

It is not possible to obtain a complete picture of the overall effect of the introduction of a bright light into an area where insects are flying without considering whether, as insects are not attracted to light, they may be repelled

by it. Here evidence is very scanty, and it is difficult to devise an experiment which will establish the truth either way. Such observations as we have been able to make lead us to believe that moths will avoid a lighted area if they can. For example, if a moth, in its approach to a light, flies into an area of shadow it will usually make an abrupt turn and fly away from the lamp. Again, if a lamp is operated in a large open space, it is possible to observe, in favourable conditions, an annular area many yards from the lamp in which insects entering the area at low velocity seem undecided and flutter about for some considerable time before flying away. On a still night, when many insects are flying, this ring of fluttering insects is very apparent.

These are, of course, mere pointers, and are not evidence that the insects observed would not behave in the same way in the absence of the light. There is, however, one rather significant observation which has been made many times by collectors working with lights. When a lamp is first lit in, for instance, a clearing in a wood, an initial batch of insects appears and, after a few minutes, the number rapidly falls off, until a comparatively steady number of arrivals is reached. If the lamp is now extinguished for a short time and re-lit, another batch makes its appearance and the process of attrition is repeated.

This behaviour can be explained by considering the light of the lamp as setting up a barrier around the lamp in the first instance, this barrier being then penetrated only by those insects whose inertia is sufficient to bring them through it before the reaction of repulsion has time to operate. The remaining insects congregate at the barrier and are turned away. When the lamp is extinguished the barrier collapses, the area refills with insects and, on lighting the lamp, the process is repeated.

We are still carrying out experiments with regularly occulting lights to try and ascertain how much of this behaviour is due to inhibition and how much to repulsion. We feel that there is enough evidence of repulsion to include it, tentatively, as a factor in general behaviour.

Taking, then, these three factors of dazzle, inhibition and repulsion into account, we have a fairly comprehensive picture of what happens around a lamp in an area where insects are flying.

The eyes of the insects will be in the sensitive condition. There will be a tendency, in the first place, to avoid the lighted area. This tendency, if it operates rapidly enough and at a sufficient distance, will cause the insect to go somewhere else. If, however, the insect has reached an appropriate distance from the lamp, by the time repulsion comes into play it will be unable to go away and will be diverted to the lamp. During the period between entering the area and reaching the lamp the eyes will have commenced to become desensitized and the insect will, if the lapse of time in its passage to the lamp is sufficient, settle before reaching it. If the time is sufficiently short the insects will make one or more transits of the lamp. It is to be expected that settlement will take place more often in the case of light, slow-flying insects than heavier insects of considerable velocity, and similar considerations arise in connection with the repulsion reaction.

This expectation is borne out in practice. As the improvement of lamp and trap is increased, so is the total number of insects taken, but the number of slow insects (e.g., GEOMETRAE) increases less rapidly than the number of fast insects (e.g., NOCTUAE).

4. SUMMARY.

1. The normal insect night flight over an area is modified by the introduction of a light-source into the area in the following ways :

 (*a*) Repulsion causes the total flight into the area to be reduced.

 (*b*) Dazzle causes a concentration of insects at the light-source.

 (*c*) Inhibition causes settling of a number of insects within the area.

2. The area over which repulsion and inhibition take place is governed by the power of the light-source.

3. The area over which dazzle takes place is governed by the surface brilliance of the light-source.

4. The power and brilliance of lamps must, for purposes of comparison, be determined in the scale of insect vision.

5. There is no evidence that any insects which would not have entered the area in their normal flight will be induced to do so by the introduction of a lamp of any known type.

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THE EFFECTS OF INFECTION WITH *NOSEMA APIS* ON THE PHARYNGEAL SALIVARY GLANDS OF THE WORKER HONEY-BEE.

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INTRODUCTION.

THE paired pharyngeal salivary or " brood-food " glands, which secrete the highly nitrogenous brood-food for the youngest larvae in the colony, lie in the anterior part of the head capsule on the dorsal surface of the brain. Each gland consists of a number of lobes and lobules ; the two main collecting ducts open into the pharynx through the pharyngeal plate.

METHODS.

A large number of worker honey-bees which had just emerged from their cells in a comb that had been kept in an incubator at 33° C. and 40 per cent. relative humidity were divided into three groups. Bees in the first group were dissected immediately in order to determine the size of their pharyngeal glands on emergence. Bees of the second group were fed individually with sugar syrup containing viable spores of *N. apis* and were subsequently marked with red paint, so that they could be recognized again, and introduced into a colony of bees known to be infected with *Nosema*. Bees of the third group were fed with pure, uncontaminated, sugar syrup, marked white, and introduced into a healthy colony of bees.

The following day further bees that had emerged within the previous twenty-four hours were divided into two groups. The bees of the first group were fed individually with syrup containing viable spores, marked pink, and introduced into the colony suffering from *Nosema* disease. Bees of the second group were fed with uncontaminated syrup, marked blue, and introduced into the healthy colony.

Nine, fifteen and twenty-one days after the experimental bees had emerged, twenty of the bees belonging to the group that had been infected with *N. apis* and twenty bees of the same age of the control, uninfected group, were collected from the colonies in which they had been placed and their pharyngeal glands were removed and measured.

RESULTS AND CONCLUSIONS.

The size of a number of lobes of pharyngeal glands taken from newly emerged healthy bees, from healthy bees nine, fifteen and twenty-one days of age, and from bees of nine, fifteen and twenty-one days of age that had been infected on the first day of adult life with *N. apis* is shown in Tables I and II.

TABLE I.—*Showing the size of the lobes of the pharyngeal glands of:* (A) *newly emerged adult worker Honey-bees ;* (B) *Healthy Bees nine days of age ;* (C) *Bees of nine days of age that had been infected with* N. apis *on their first Day of adult life.*

No. of bees.	Group (A) : Newly emerged adult-bees (20 individuals).		Group (B) : Healthy bees nine days old (20 individuals).		Group (c): Bees nine days old infected with N. apis (20 individuals).	
	No. of lobes measured.	Mean length of lobes measured.	No. of lobes measured.	Mean length of lobes measured.	No. of lobes measured.	Mean length of lobes measured.
1	32	46	64	220·3	49	96·4
2	43	43	53	209·6	56	110·5
3	60	52	55	200·3	50	104·3
4	22	55	39	207·1	39	97·0
5	36	46	42	192·2	35	103·6
6	24	50	39	198·5	29	112·3
7	41	55	43	197·0	56	121·1
8	29	42	44	199·3	34	91·4
9	36	50	64	230·7	59	100·6
10	21	45	43	194·0	50	116·0
11	23	47	59	223·4	42	111·4
12	27	50	70	214·3	40	117·6
13	24	54	45	207·2	45	104·3
14	19	49	26	198·6	45	111·1
15	26	50	39	190·1	60	94·4
16	29	52	41	238·3	53	99·1
17	32	49	36	197·1	50	103·0
18	25	49	31	195·4	35	109·4
19	23	50	25	194·6	25	114·3
20	24	52	32	202·9	34	118·2
Totals	592	570	890	4110·7	887	2136·0
Mean of means		48·5μ		205·53μ		106·8μ

In Table III the mean length of the lobes of the pharyngeal glands of healthy and diseased bees of these three different age groups, and of newly emerged healthy bees, has been extracted from Tables I and II.

TABLE III.—*Showing the Mean Length of the lobes of the pharyngeal glands of healthy, newly emerged, adult Bees ; healthy Bees nine, fifteen and twenty-one days of age ; Bees nine, fifteen and twenty-one days of age that had been infected with* N. apis *on the first day of adult life.*

Age group of bee (days).	Healthy bees. Mean length (μ) of lobes of pharyngeal gland.	Bees infected with N. apis on 1st day of adult life. Mean length (μ) of lobes of pharyngeal gland.
1st day	48·5μ	
9th ,,	205·2μ	106·8μ
15th ,,	127·9μ	76·3μ
21st ,,	86·7μ	72·2μ

From these figures it is clear that infection with *N. apis* has a considerable influence on the size of the lobes of the pharyngeal glands of the adult worker

TABLE II.—*Showing the size of the lobes of the pharyngeal gland of:* (A) *Healthy Bees fifteen days of age that had been infected with* N. apis *on their first day of adult life;* (B) *Bees of fifteen days of age that had been infected with* N. apis *on their first day of adult life;* (C) *Healthy Bees twenty-one days of age;* (D) *Bees of twenty-one days of age that had been infected with* N. apis *on their first day of adult life.*

No. of bees.	Group (A): Healthy bees 15 days of age (20 individuals).		Group (B): Bees 15 days of age infected with N. apis (20 individuals).		Group (C): Healthy bees 21 days old (20 individuals).		Group (D): Bees 21 days old infected with N. apis (20 individuals).	
	No. of lobes measured.	Mean length of lobes measured (μ).	No. of lobes measured.	Mean length of lobes measured (μ).	No. of lobes measured.	Mean length of lobes measured (μ).	No. of lobes measured.	Mean length of lobes measured (μ).
1	72	131·7	57	74·8	44	95·5	64	69·3
2	53	148·4	46	81·4	42	89·8	33	68·2
3	52	117·3	62	74·3	50	85·4	45	81·4
4	30	122·6	31	76·5	42	84·3	63	67·5
5	26	120·9	42	85·4	41	89·7	39	69·7
6	41	129·6	31	79·2	52	96·9	44	70·4
7	36	158·6	26	73·3	55	94·4	64	87·6
8	25	139·7	24	91·6	41	92·7	41	65·5
9	67	128·0	30	73·3	55	83·7	52	75·9
10	31	112·6	42	69·9	39	86·5	62	65·2
11	25	115·3	46	80·1	40	85·7	41	69·3
12	36	120·6	48	75·4	52	112·2	26	77·4
13	14	118·3	45	74·6	53	55·2	39	75·3
14	28	137·6	61	69·2	45	77·9	40	68·1
15	35	122·3	20	73·7	50	78·4	32	73·4
16	41	125·6	24	77·9	52	84·9	30	72·1
17	53	141·2	19	79·3	42	87·3	25	69·3
18	21	129·6	25	76·1	45	80·4	36	70·3
19	33	125·2	28	67·3	50	81·4	41	72·5
20	19	112·9	26	73·3	49	94·9	39	75·2
Totals	738	2558·0	733	1526·6	939	1734·2	856	1444·0
Mean of means		127·9μ		76·33μ		86·7μ		72·2μ

honey bee. A serious reduction in the amount of brood food secreted must result during that period of the adult bee's life, from the ninth to the fifteenth day after emergence, when she is normally concerned with feeding the youngest larvae in the hive on this secretion. This effect of *N. apis* on the pharyngeal glands of the worker honey bee is graphically shown in the photograph (Plate 1).

There can be no doubt that the diminution in the quantity of brood-food produced by young bees infected with *N. apis* must upset considerably the economy of the colony to which they belong. So serious was this effect considered to be that it was decided to make a more comprehensive study of the state of development of the pharyngeal glands of healthy and *Nosema* infected bees.

Method.

A large number of bees that had very recently emerged from a brood comb that had been kept in an incubator at 33° C. was divided into two groups. Bees of the first group were marked red and fed for two days in cages on syrup in which a large number of viable spores of *N. apis* were suspended ; after two days these bees were introduced into a colony suffering from *Nosema* disease. Bees of the second group were fed on uncontaminated syrup, marked white, and after two days introduced into a healthy colony of bees.

At intervals a number of bees belonging to the healthy group and a number of bees belonging to the infected group were removed from their respective colonies, and the state of development of their pharyngeal glands determined using the criteria first employed by Soudek (1927), viz. :

A. *Full :* Glands secreting freely ; lobes very distended and covering the main duct completely.

B. *Diminished :* Glands secreting but lobes not fully distended, and main duct not completely covered.

C. *Empty :* Glands not secreting ; lobes small, main duct freely exposed.

D. *Atrophied :* Glands not functioning ; lobes very small, often rendering it difficult to determine their outlines with any degree of precision.

Results.

The results obtained in these investigations are shown in Table IV.

From this it will be seen that, under the conditions of this experiment, approximately 66 per cent. of the healthy bees had fully functional pharyngeal glands by the seventh day of adult life, and that by the tenth day of adult life 100 per cent. possessed fully functional glands. This condition persisted until the fourteenth day of adult life, by which time a reduction in the degree of activity of the pharyngeal glands had become apparent. Thereafter the degree of activity decreased steadily and rapidly until, by about the twentieth day of adult life, very few bees possessed glands that were actively secreting brood-food.

In the case of the bees that were experimentally infected with *N. apis* during the first two days of adult life, none had glands that were secreting brood-food really actively by the seventh day of adult life ; after the seventh day a progressive and rapid decline in the degree of secretory activity of the pharyngeal salivary glands became apparent until, by the thirteenth or fourteenth day of adult life, these glands had atrophied.

TABLE IV.—*Showing the degree of secretory activity of the pharyngeal salivary glands of healthy and* Nosema *infected worker Honey-bees of different ages.*

Healthy bees.

Age of bees in days.	No. of individual bees examined.	Degree of activity of pharyngeal glands.			
		Full.	Diminished.	Empty.	Atrophied.
7	12	8	3	1	0
9	15	14	1	0	0
10	10	10	0	0	0
12	14	14	0	0	0
13	10	10	0	0	0
14	15	13	2	0	0
15	10	9	1	0	0
18	12	4	8	0	0
20	14	1	10	3	0
22	10	0	4	6	0
24	12	0	2	9	1
26	10	0	2	3	5

Bees infected with *Nosema apis.*

Age of bees in days.	No. of individual bees examined.	Degree of activity of pharyngeal glands.			
		Full.	Diminished.	Empty.	Atrophied.
7	14	0	4	5	5
9	11	0	1	2	8
10	14	0	0	2	12
12	15	0	0	3	12
13	11	0	0	1	10
14	16	0	0	0	16
15	9	0	0	0	9
18	10	0	0	0	10
20	6	0	0	0	6
22	8	0	0	0	8
24	4	0	0	0	4
26	.	.	.	.	.

It would therefore appear that infection with *Nosema apis* during the first few days of adult life—that is to say just at that time when the young worker honey-bee is actively engaged in cell cleaning, and is therefore most likely to become infected by working wax that has been contaminated with faeces of older workers containing viable spores—has a most deleterious effect upon the subsequent development of the pharyngeal salivary glands and, as a direct consequence, on the ability of the bees concerned to produce the brood-food with which to feed the youngest larvae in the hive. Should many young bees in a colony become affected in this way it cannot but have a very harmful effect upon the future development of the colony and, in serious cases, may well lead to the death of the colony concerned.

SUMMARY.

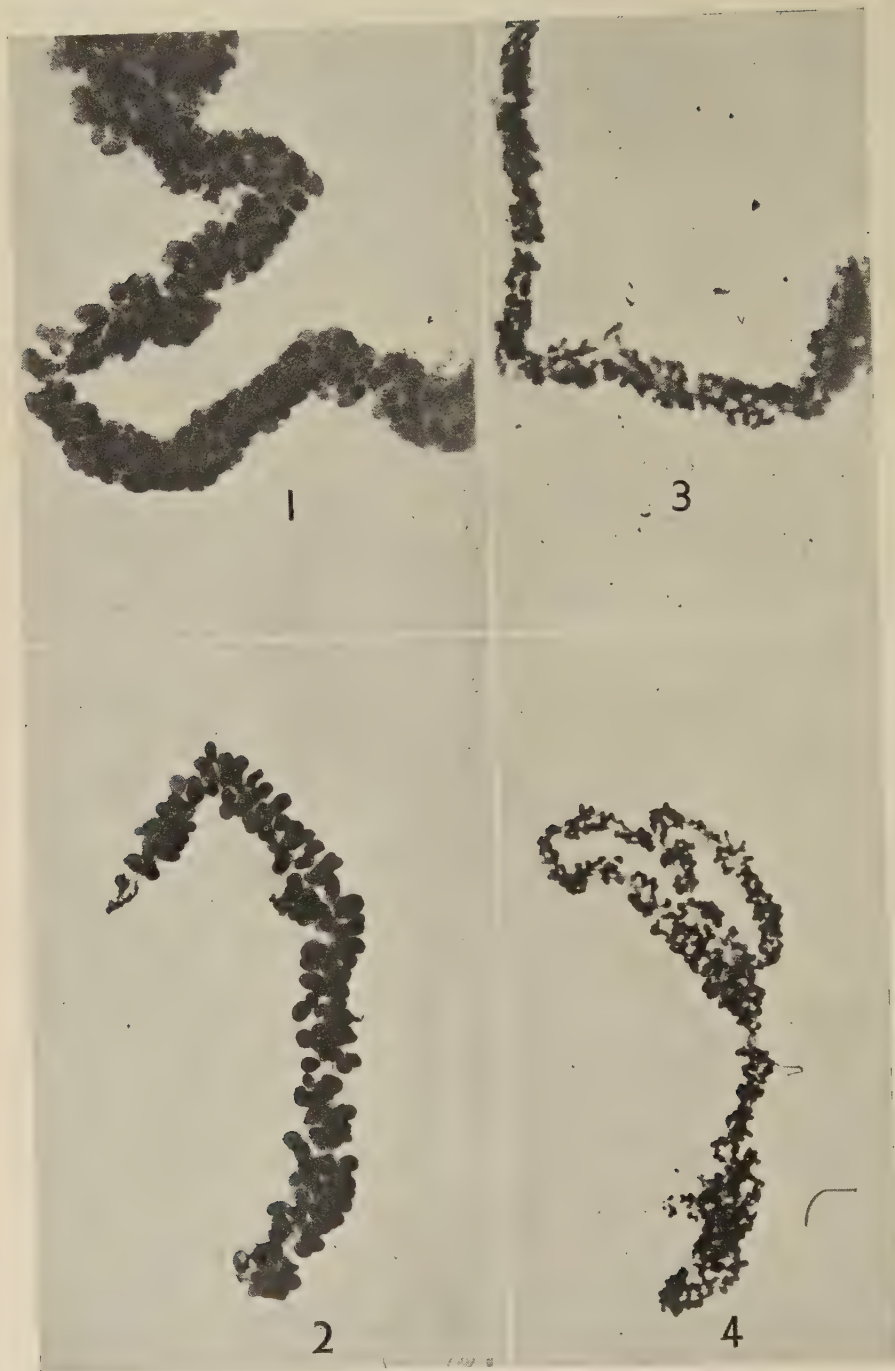1. Infection with *Nosema apis* has a considerable influence on the size of the lobes of the pharyngeal glands of the adult worker honey-bee.

2. Infection with *N. apis* during the first few days of adult life has a most deleterious effect upon the bees concerned in producing the brood food for the youngest larvae in the hive.

Plate 1.

Pharyngeal salivary glands of healthy and diseased bees.

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PLATE I.

Photograph showing a portion of the pharyngeal salivary glands of (1) a healthy bee 9 days old ; (2) a healthy bee 15 days old ; (3) an infected bee 9 days old ; (4) an infected bee 15 days old.

BOOK NOTICES.

Nordens Eupithecier : en udførlig Behandling af de i Fennoskandia og Danmark forekommende Eupitheciae Curt. By KNUD JUUL. 8vo. Aarhus (Andersen), 1951. Pp. 147, 13 pls. (6 col.), maps. Price 34*s*. (In Danish, with short descriptions in English.)

Fifty-six species of the Geometrid genera *Eupithecia, Gymnoscelis* and *Chloroclystis* are described, with distribution maps of Denmark, and a small sketch of the fore wing of each species. For each there is also an abbreviated description in English of the moth, caterpillar, and chrysalis, and notes on distribution and time of flight.

There are tables of distribution for Norway, Sweden and Finland, with key maps. An analytical table gives occurrences and food-plants month by month. Six plates, three of larvae and three of adults, are coloured ; the remaining plates are occupied by figures of the male genitalia of nearly all the species.

Insects as Human Food : a Chapter of the Ecology of Man. By F. S. BODEN-HEIMER. 8vo. The Hague (Junk), 1951. Pp. 352, 47 figs. Price 10 Dutch Guilders.

A study on the thesis that insects are not merely an occasional item, but an integral part of the diet of primitive peoples. After a general survey and an estimation of the nutritive value of insect food, there is a historical account of entomophagy from antiquity to the present day in Europe, and a chapter on each of the other continents surveys the edible insects peculiar to each. There is a long bibliography of twenty pages, which the author modestly states is incomplete.

OCCURRENCE OF COLLEMBOLA IN THE AIR.

By J. A. FREEMAN, PH.D.

THE following records of Collembola collected in the air are of interest with reference to the discussion on Dr. J. T. Salmon's paper, "The Role of Collembola in Zoogeography" given at the Royal Entomological Society's meeting on 2nd May, 1951 (1951, *Proc. R. ent. Soc. Lond.* (C) **16** : 18) :

(*a*) Berland (1935–37), collecting by tow-nets from aeroplanes near Paris. took Collembola at heights up to 2000 metres.

(*b*) Glick (1939), working in the Southern States of the U.S.A., collected Collembola from 200 to 11,000 ft. The method of collection, by sticky traps on aircraft, made it impossible to determine whether the insects were alive or dead when collected. The 26 specimens taken were identified as follows : PODURIDAE : *Onychiurus* sp. ; ENTOMOBRYIDAE : *Entomobra multifasciata* Tullgren, *Entomobra* sp., *Sira nigromaculata* Lubbock, *Orchesilla ainslei* Folsom, *Tomocerus flavescens* Tullgren var. *americanus* Schött ; SMINTHURIDAE : *Bourlettia* sp., *Sminthurus* sp.

(*c*) Freeman (1945) collected living Collembola in nets flown from wireless masts at Tetney, Lincs., in 1934–35. Collections were made at heights of 277 ft., 177 ft. and 10 ft. above the ground. Detailed records, not given in the paper cited, are as follows :

Nets at 277 ft.   5 specimens on 3 occasions.
    ,,   177 ft.   4   ,,   4   ,,
    ,,   10 ft.   4   ,,   1 occasion.

These records are sufficient evidence that living Collembola are carried by wind currents, and are neither more nor less subject to drying up than other similar sized components of the aerial fauna.

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GLICK, P. A., 1939, The distribution of insects, spiders and mites in the air. *Tech. Bull. U.S. Dep. Agric.* **673**.

REPRODUCTION IN THE HOUSEFLY (*MUSCA DOMESTICA* L.).

By Ursula M. Hampton.

(*London School of Hygiene and Tropical Medicine.*)

THE following study was undertaken in order to determine the effects of the presence of males on the reproductive and general physiology of the female housefly (*Musca domestica* L.).

It has long been known that the female is fertilized for life by a single copulation ; experiments were designed to determine whether the male has any subsidiary effect on the female. In the first experiment the effect of the presence or absence of a male on the reproductive behaviour of a female was investigated and, in the second, such differences as had been found were further analysed.

Experiment 1 : *Stimulation of a Female by the Presence of a Male.*

Copulation of a virgin fly lasts longer than thirty minutes and may last for two hours, about one and a half hours being the most usual time ; more than 50 observations have been made. Short copulations, in which the male alights on the female, caresses the head and moves backwards, bringing the genital apertures of the two flies together and then leaves her, only occur in young, immature females, or those which have already been fertilized. In these " pseudo-copulations " the ovipositor is never exserted. A male fly may alight on a mature virgin female, caress her head and then leave, but only to return very soon. After moving backwards to the copulating position a male was not seen to leave a mature virgin female without copulation ; that is to say " pseudo-copulation " does not occur in mature virgin flies.

The larvae were fed on moistened guinea-pig meal[1] : extra moisture at the time of pupation induced migration into the surrounding sand. Medium-sized pupae were selected because the largest produced a high percentage of females and the smallest a high percentage of males. The pupae were isolated in tubes in which the flies emerged : these were then used as required.

The flies were kept in cages 6 in. $\times$ 6 in. $\times$ 6 in. made from a wire frame covered with a sleeve of mosquito netting. Eggs were deposited on cotton-wool pads moistened with milk and water.

There were three series of flies. In series 1 a single female was kept with one male ; in series 2 one female was kept with one male, which was removed after the first batch of eggs had been laid ; in series 3 one virgin female was kept alone. Data were recorded on the pre-oviposition period, frequency of laying eggs (days of life/total number of batches), total number of batches, total number of eggs.

Series 1 (normal pairs) does not differ significantly in any way from series 2 (fertilized female). Table I gives results for series 1 ; it is unnecessary to give data for series 2, in which 12 females were observed.

[1] Analysis gives the following proportions :

Animal protein . . . 5%	Dried yeast . . .	3%
Dried milk products . . 10%	Salt . . .	0·5%
Vitamix 15%	Yellow maize meal . .	35%
Dried grass meal . . . 2%	Wheat feed . . .	20%
Arachis oil 5%	Water	4·5%

TABLE I.—*Series* 1 : *Records from* 12 *normal pairs of flies.*

Pre-oviposition period (days).	Frequency = life/ batches.	Total batches.	Total eggs.	Average eggs/batch.	Life of ♀ (days).
5·0	2·4	9	1191	132·3	22
4·5	2·7	11	889	80·3	30
4·0	2·7	8	628	78·5	22
4·5	2·8	11	972	88·3	31
5·0	3·0	12	1278	106·5	36
4·0	3·0	6	673	112·1	18
5·0	3·3	7	848	121·1	23
4·5	3·4	8	676	84·5	27
4·0	3·4	7	738	105·4	24
4·0	3·8	6	577	96·2	23
4·5	4·1	7	578	·82·7	29
4·5	5·0	6	606	101·0	30
Means: 4·46	3·3	8	805	99·1	26·3

Virgin flies lay fewer batches, fewer eggs, have a longer pre-oviposition period and lay less frequently than fertilized flies. The length of life does not differ significantly in these two groups, but it tends to be prolonged if fertilization is delayed until late in life. Table II gives results for virgin flies.

TABLE II.—*Series* 3 : *Individual records of* 20 *virgin females.*

Pre-oviposition period (days).	Frequency = life/ batches.	Total batches.	Total eggs.	Average eggs/batch.	Life (days).
5	6·0	1	139	139·0	6
14	6·0	4	364	91·0	24
5	4·3	6	435	72·5	26
5	6·3	4	242	60·5	25
13	8·7	3	484	161·3	26
8	9·0	1	97	97·0	9
15	9·0	3	246	82·0	27
16	9·3	3	254	84·7	28
6	10·0	1	127	127·0	10
9	10·5	2	226	113·0	21
14	11·5	2	284	142·0	23
16	12·5	2	145	72·5	25
13	13·5	2	191	95·5	27
15	20·0	1	121	121·0	20
18	21·0	1	140	140·0	21
20	23·0	1	44	44·0	23
14	25·0	1	123	123·0	25
		0	0	0	9
		0	0	0	20
		0	0	·0	21
Means : 12·1	12·1	1·9	183·1	88·3	20·8

In virgin flies there is no inhibition of the initial maturation of the eggs, but many virgin flies seemed to die because they were egg-bound. Table III shows the conditions at death of virgin and fertilized flies.

The experiment shows that there is a marked difference between fertilized and virgin flies, but that, after copulation has occurred, the presence of a male does not affect the female. The "pseudo-copulation" in fertilized females described in the first paragraph does not stimulate the female throughout her life.

Table III.—*Condition of the ovaries at death of fertilized and virgin females.*

	Number dissected.	Number with eggs.	Per cent. with eggs.
Series 1 : Normal pairs . .	9	4	44
Series 2 : Fertilized ♀ without ♂	7	3	43
Series 3 : Virgin females . .	11	10	91

Experiment 2 : Testis Implantation.

The differences which have been described might be due to the presence of spermatozoa in the female, to the presence of some other substance produced by the testes, or to physiological effects of the copulation. The first of these possibilities was tested by implanting ripe testes into the thoracic muscles of a virgin fly and comparing the number of eggs laid with that laid by normal virgin flies. The flies were frozen, fastened to a slide with plasticine, and then one or more testes were inserted through a hole cut in the thoracic muscles. The hole was sealed with cellodin.

Table IV gives the results for " control operated " flies, i.e., those in which a hole was cut in the thorax but no testis was implanted, and for flies with one testis and with six testes implanted. If these means are compared with the means for normal virgins (Table II) it will be seen that there are several differences, the most marked being the shortened pre-oviposition period and increased frequency of laying.

Table IV.—*Means of individual records after different treatments.*

	Pre-oviposition period (days).	Frequency = life/batches.	Total batches.	Total eggs.	Average eggs/batch.	Life (days).
Control operated (18 flies) .	8·66	8·175	2·35	199·25	74·92	17·05
Operated one testis (23 flies) .	9·87	9·876	1·86	158·2	69·18	16·60
Operated six testes (10 flies) .	8·5	9·76	1·545	138·2	78·47	13·80
Fertilized ♀♀ (12 flies) .	4·46	3·28	8·16	804·5	99·09	26·2
Normal virgins	12·1	12·1	1·9	183·1	88·3	20·8

In Table V those differences which are significant are listed. There are no significant differences between flies with testes implanted and " control

Table V.—*Significant differences between the three groups of flies and normal virgin flies.*

		Significance level.
Control operated .	Preoviposition period . .	5%
	Life (days) . . .	5%
	Frequency	5%
One testis . .	Preoviposition . . .	6%
	Eggs/batch . . .	5%
	Life (days) . . .	5%
Six testes . .	Preoviposition . .	5%
	Life (days) . . .	5%

operated " flies ; all significant differences are between operated flies and normal virgin flies. One concludes that the operation shortens life and shortens pre-oviposition period.

Since the number of batches does not differ between the operated and normal virgin flies, and life is shorter, one would expect batches to be laid more frequently in the operated flies. This was not so, however, except in the comparison between control operated and normal flies : frequency was greater in the control operated (Table IV). Flies with one testis implanted lay fewer eggs per batch than normal virgin flies (Table IV). This is not easily explained ; it is difficult to see why this group (one testis) only should have a lower average yield than both the normal flies and the flies with six testes implanted.

Transplanting testes into virgin female flies does not affect their egg laying, as shown by these experiments. Many of the flies were dissected after death and the remains of the testis was found in only a few.

The important fact which arises is that the pre-oviposition period is shortened by stimulating the fly by operation : it is not reduced to the period of normal *fertilized* flies, which is 4–5 days.

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THE AWAKENING AND DIURNAL FLIGHT ACTIVITIES OF VESPINE WASPS.

By Albro T. Gaul.

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It was noted that while wasps were asleep in their cages at night, they could be easily awakened by turning on a light. Moreover, their periods of flight could be completely controlled by alternately turning the light on and off. It was thus discovered that wasps could not fly in darkness. This led directly to a consideration of the factors which influence the diurnal behaviour of these wasps.

Work was done during the summer of 1949 with colonies of *Vespula maculifrons* Buy. The first awakening observations were made on 17 August, 1949, when the author collected data on wasp flights as they related to time and light intensity. Illumination was determined with a standard foot-candle meter, the accuracy of which was previously checked with the manufacturer. Data were collected from 5.00 a.m. before the wasps awakened, until 9.00 a.m. when the colony was fully active.

Wasp activity was described in terms of total flights per minute, both toward and away from the nest. This was found to be a very satisfactory method of checking the activity of the colony, since 50 per cent. or more of the workers engage in labours afield. Recording the total flights was more accurate than recording only unidirectional flights for reasons to be developed later in this paper.

The results of similar observations made on 18th and 19th August were most unsatisfactory when superimposed on a single set of co-ordinates of which the ordinate was flights per minute and the abscissa was foot-candles of light. There was no common starting point, nor indeed any similarity between the curves obtained.

Early morning observations made from 20th August to 2nd September, however, included data on temperature as well as light intensity, flights and time. As before, plotting flights per minute against temperature, against time or against foot-candles showed a meaningless jumble of curves. It was noted, however, that *V. maculifrons* never awakened when the light intensity was below 0·5 foot candles, nor when the temperature was below 8·5° C. It was therefore surmised that there might be a double and interdependent threshold of stimulus for flight in the form of temperature and light.

Consequently a curve, fig. 1, was prepared on which the ordinate was in degrees centigrade while the abscissa was foot candles. The points on this co-ordinate system were the awakening points of the colony.

The point of colony awakening was taken as that moment when the wasps were flying at the rate of two flights per minute and beyond which moment that rate was sustained. Observations on other colonies of the same species showed identical awakening points.

The mathematical representation of this curve may be expressed as the equation : $U_X = \cdot 93X^4 - 18\cdot 80X^3 + 112\cdot 45X^2 - 193\cdot 76X + 363\cdot 27$, when light is in foot candles and temperature is in degrees absolute.

It was thought necessary to give some consideration to the more or less arbitrary standard of two flights per minute as the colony awakening point. By counting early morning stragglers who fly prior to threshold conditions the following facts were discovered : These wasps fly *into* the nest before threshold conditions at the rate of 2–3 every four minutes, and since they fly into the nest they do not represent colony awakening.   Thus if the number of flights attains the rate of 2 per minute, and this rate is sustained or increased, it means that wasps must be flying from the nest in order to attain this rate, and hence the colony must be in the process of waking up for the day.   Therefore this standard of two flights per minute as an awakening point is really significant and is a useful standard.
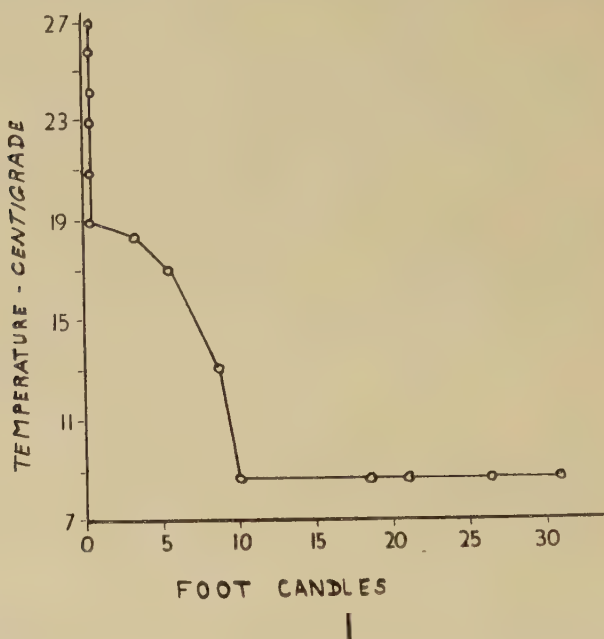

FIG. 1.—*V. maculifrons* awakening points, 20th August to 2nd September, 1949.

The incoming wasps are accounted for by the fact that they are overtaken by darkness and spend the night out of the nest.   When conditions at their individual resting places reach threshold for flight they fly to the mother nest. This does not mean that conditions are at threshold for flight at the nest site.

Since the instruments were not located at the precise location of the nests, (being located about 6 ft. from the nest cages) it was necessary to determine the deviation between the readings at the instrument locations and the nest site.   A thermometer was thrust into the nest entrance (a tube through the earth excavated by this subterranean species).   This thermometer registered the same temperature as the thermometer at the regular reference point.   It was thus assumed that there was little significant error in the temperature readings.

Since the light meter was also located at the same distance from the nests, its readings were compared at the nest entrance and at the regular reference point.

The variations in these comparisons were consistent at —0·2 foot candles, which was less than the calibration points on the meter scale.

It was next necessary to determine if the standard of two flights per minute was actually indicative of colony awakening, or whether it was the result of previous activity within the nest. On three consecutive mornings the author made close-up inspections of the nest prior to flight threshold conditions. About ten minutes before flight with the temperature already above threshold a few wasps moved stiffly about. This action is accompanied by desultory cleaning and wing fluttering. Dotterweich (2) and Bachmetjew (1) have shown that the early morning or late evening fluttering of wings (among Lepidoptera) is probably useful in raising the temperature of the wing muscles by metabolic action so that the wings can function at flight frequencies. It is possible that this early morning fluttering may be of similar use to the wasps. It has been noted, however, that the fluttering individuals are not necessarily the first ones to fly. Moreover, the temperature has already been observed to be above threshold. The author, therefore, interprets this pre-flight fluttering as a response to the returning stragglers who tread indiscriminately upon their sleeping sisters. It is also possible that this behaviour may be a simple response equivalent to yawning and stretching upon awakening among mammals.

It was thus impossible to make an exact determination whether these actions were a pre-flight awakening or a simple response to a disturbance. Since many wasps did not indulge in any awakening activity until they walked to the nest entrance to take flight, it was concluded that the standard of 2 flights per minute was as accurate a determination of colonial awakening as any that could be devised with present equipment and knowledge. (Smaller colonies with smaller populations would necessarily have different awakening flight rate standards, etc.).

From 20th August to 2nd September similar data were collected in the evenings as the wasps entered the nest for the night. A typical curve of the incidence of evening flights is shown as part of fig. 2. In the evening the light intensity decreases more rapidly than the temperature, therefore the change in rate of flight is directly related to the light intensity. With this fact in mind it was interesting to note that all flights came to a halt at 0·5° C., the exact morning threshold.

As the light decreases below 100 foot-candles the number of flights begins to decline. At *circa* 25 foot-candles there is a sudden surge of returning workers, which temporarily increases the total flight rate, even though the number of outgoing flights continues to decline. This flight of returning workers endures for about one half hour, after which the colony activities close for the day. Because of this phenomenon the total counts per minute render a more accurate index of colony activity than the counting of only unidirectional flights.

On the evening of 27th August, after the wasps had retired for the night, and before the temperature had dropped below the threshold for flight, a 100-watt tungsten lamp was turned on near the nests. In a few moments several wasps had emerged from the nests and were buzzing about the light. This clearly indicates that the light is a basic factor in waking and sleeping responses. The following night, after the temperature had fallen below the threshold point, the experiment was repeated. No wasps attempted flight.

It is probable that these thresholds are fairly constant during the entire colony season. They may even establish the points at which queens in hibernation will begin to fly on warm winter days as noted by Duncan (3) and others.

It has been noted that seasonal wasp abundance is correlated with spring weather. Fox-Wilson (4) has been only partially successful in relating wasp abundance to spring rainfull. No doubt light and temperature thresholds would affect the queens in selecting their nesting sites. There is at present no evidence of any kind on the flight thresholds for queens of any species ; however, it is reasonable to believe that such thresholds must exist.

Fig. 2 represents a daily flight graph for 22nd August. It is fairly typical of the flight curve obtained during any day of continuous good weather. It will be observed that the number of flights increases rapidly after the first awakening. The flights again decrease to a daily normal after the first $2\frac{1}{2}$ hours. The daily normal continues unbroken until sunset, when the evening activities, already considered, are begun.

The rapid early morning rise above the daily normal may be caused by one or more of several factors :

(1) After a night without food the larval food requirements may have increased, with a subsequent increase in the labour demands of the colony. This may increase the rate of flights until the demand is filled.

(2) These early flights may be exercise flights for the wasps who remain largely within the nest as brood nurses.

(3) Many of these early morning flights may be for the purpose of releasing wastes which have accumulated during the night. This would force the brood nurses and others to make flights at this time.

Considerable evidence was collected on the diurnal activities of *Dolichovespula maculata* Linnaeus and *Polistes fuscatus* Fabricius. *D. maculata* is an arboreal species with a more northerly range of distribution, and could be expected to have a much lower temperature threshold for flight. This is true. The graph of its awakening points is identical in its configuration to that of *V. maculifrons*, but its thresholds have been established at 5° C. and 0·25 footcandles. *Polistes* on the other hand is a northerly element of a successful neotropical genus and has a much higher temperature threshold. Attempts to determine its flight thresholds were impossible in western Massachusetts, where the light increases much more rapidly than the temperature.

Reference to fig. 2 will show that the curve of daily activities in terms of flights per minute indicates not only when certain phenomena occur, but that it also shows the quantity of flights. Up to the present it has been impossible to determine the regular labour output of a colony. A mathematical treatment of the curve by Simpson's equation demonstrates that there were no less than 22,500 flights from the one nest on 22nd August. Since these were two directional counts, there were 11,250 round trip flights. On other sunny days this nest registered from 10,000 to 14,000 such flights.

Some of these figures were obtained by direct count of the flying insects. Errors in this technique involve the time needed to glance at a clock, during which moment some wasps may not get counted. Other counts were made with a photo-electric electronic timer-counter. With this instrument one encounters the error of coincident wasps being counted as one wasp. The great advantage of the counter was that it was automatic and could leave the author

free for other research. Over a series of tests, the direct observational count was compared with simultaneous electronic count. Apparently the errors of both methods were identical, since tallies yielded the same total counts.

Returning to the figures obtained from fig. 2, there were 260 ergates in the colony on 22nd August. Therefore the average number of flights per wasp on that day was 43·6 round trips (11,250/260). Since there were 14·5 flying hours in that day the average wasp made one round trip each 20 minutes.
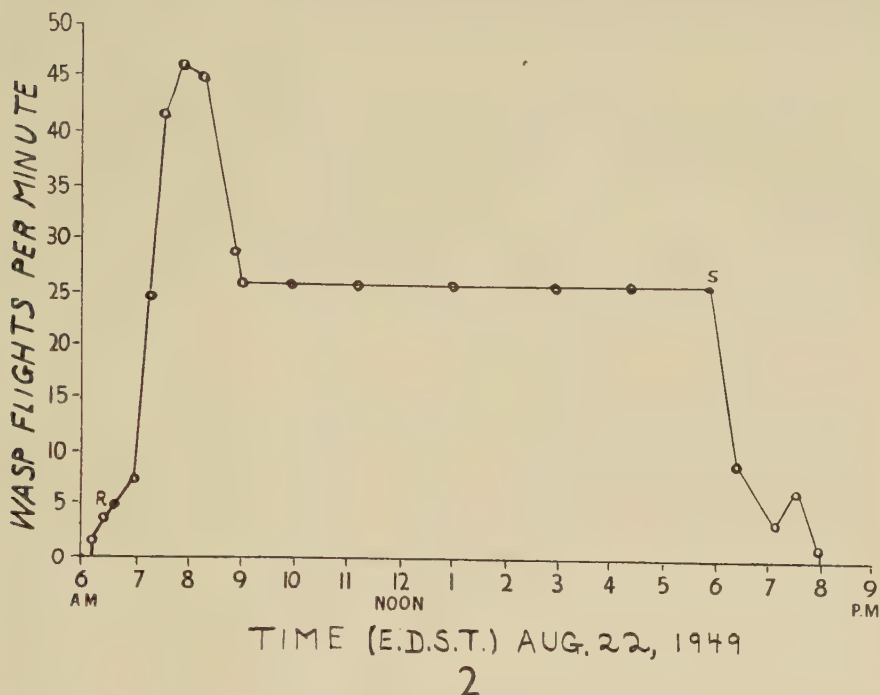

FIG. 2.—A typical daily flight chart of *V. maculifrons.* R is point of apparent sunrise; S point of apparent sunset.

I have elsewhere described the division of labour in the typical Vespine colony (5). In that paper it was shown that nearly 50 per cent. of the workers remain within the nest during most of the day, serving either as brood nurses, nurses for the teneral adults, etc. Therefore the average flying wasp probably makes many more than 43·6 round trips per day. An estimate of one round trip every ten minutes is very reasonable, as the author has previously recorded nest repair workers making round flight trips every four minutes (6).

SUMMARY.

It can be stated that wasps are awakened in the morning when both light and temperature reach certain threshold conditions which seem specific for each wasp species. These thresholds may influence the early activities of the queens in the spring, and hence may be factors in controlling wasp abundance. The evaluation of colony activity in terms of flights per minute is useful and

empirically justifiable. A very reasonable estimate of wasp labour output can be made on the basis of knowing the total number of flights per day, colony census, and distribution of labour.

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(1) BACHMETJEW, P., 1899, Über die Temperatur der Insekten nach Beobach-tungen in Bulgarien. *Z. wiss. Zool.* **66** : 521–604.

(2) DOTTERWEICH, H., 1928, Beiträge zur Nervenphysiologie der Insekten. *Zool. Jb.* (Physiol.) **44** : 399–450.

(3) DUNCAN, C. D., 1939, A contribution to the biology of North American Vespine wasps. *Stanford Univ. Publ. biol. Sci.* **8** : 1–272

(4) FOX WILSON, G., 1946, Factors affecting populations of social wasps, *Vespula* species, in England (Hymenoptera). *Proc. R. ent. Soc. Lond* (A) **21** : 17–27.

(5) GAUL, A. T., 1948, Additions to Vespine biology. V. The distribution of labor in the colonies of hornets and yellowjackets. *Bull. Brooklyn ent. Soc.* **43** : 73–79.

(6) ——, 1947, Additions to Vespine biology. III. Notes on the habits of *Vespula squamosa* Drury (Hymenoptera, VESPIDAE). *Ibid.* **42** : 87–96.

BOOK NOTICE.

Mosquito Behaviour in Relation to Malaria Transmission and Control in the Tropics. By R. C. MUIRHEAD-THOMSON. 8vo. London (Edward Arnold & Co.), 1951. Pp. viii + 219, 16 pls. Price 30s. net.

In this work an attempt is made to review the present knowledge of the behaviour of the Anopheline mosquitoes which are responsible for malaria transmission in the tropics. In his introduction the author states that he has intentionally limited himself to the additions to our knowledge which have been made during roughly the last fifteen years, which period has seen a great increase in our knowledge of this group, and has also coincided with great advances in the study of insect physiology and revolution in methods of chemical control.

The book is divided into two parts. The first is concerned with general activity and movement in relation to mating, feeding, and longevity, and the influence of external conditions. The second part discusses factors in the nature and selection of breeding places, and the part played by physical and chemical factors in determining the behaviour of the female mosquito and of the early stages.

A bibliography of the relevant literature is given at the end of each chapter.

THE STRIDULATION NOISE OF LOCUSTS.

By E. J. Evans, B.Sc.

(*Communication from the National Physical Laboratory.*)

Introduction.

This paper describes an investigation of the acoustical characteristics of the stridulation noise of *Locusta migratoria migratorioides* Reiche & Fairmaire in the gregarious phase. Oscillograms of the stridulation noise were recorded, and the sound was analysed up to a frequency of about 18,000 c.p.s. by means of an acoustic spectrometer.

The information obtained appears to be of interest to biologists in connection with the study of the production and reception of sound by the locust. The stridulation noise was found to consist of a regular succession of pairs of pulses of high-frequency sound. Results are given for the duration, rate of repetition and analysis of the pulses, and a number of typical oscillograms are reproduced.

Method of Investigation.

About 12 pairs of mature locusts were used for this investigation. They were placed in a cage, about 1 foot cube, constructed of fine copper gauze on a wooden base, the latter being covered with about three inches of sand.

The experiments were conducted in a sound-proof room lined with sound-absorbing material which practically eliminated sound reflection from the room surfaces.

(a) *Oscillograph Investigation.*

Oscillograph records were taken of the stridulation noise of the locusts by means of a small crystal microphone in conjunction with an amplifier and a double beam cathode ray oscillograph. The microphone was of a type specially designed to have a uniform response over a wide frequency range, and the overall response of the equipment was substantially level from about 100 to 18,000 c.p.s.

For the records the microphone was placed just outside the cage, about 2 inches from one of the sides. This was found to be more convenient than placing the microphone inside, where it was liable to be disturbed by the locusts, and it is not thought that the results are appreciably affected by transmission losses due to the gauze sides of the cage.

The stridulations were not very frequent, and almost invariably only one locust would stridulate at a time. The duration of a stridulation was of the order of one or two seconds, and records were taken whenever a suitable opportunity occurred, without regard to which particular locust was stridulating. The oscillograms were obtained by means of a drum camera, the exposure being started as soon as possible after the commencement of a stridulation. Some of the records were taken at a film speed of about 100 cm. per second in order to show the general sequence of pulses during a stridulation, and other records were taken at about 800 cm. per second to give the detailed wave forms of the pulses.

(b) *Analysis.*

For the analysis of the stridulation noise the equipment was modified by the substitution of an audio-frequency spectrometer for the cathode ray oscillograph. The spectrometer analyses the sound spectrum into 27 frequency bands, each about one-third octave wide, and centred about the one-third octave frequencies from 40 to 16,000 c.p.s. The spectrum is traversed 20 times per second by means of a motor-driven switch which scans the outputs of the filter circuits in the analyser. The analysis is shown up as a line spectrum on the screen of a cathode ray tube, the peak intensity in each band being indicated by the length of the corresponding line on the screen. The spectra of a number of stridulations were photographed, and the relative intensities in the bands were calculated from measurements of the photographs and the appropriate calibrations of the equipment.

RESULTS.

(a) *Oscillograph Records.*

Plate I gives typical portions of three different slow speed records. The records are probably for different locusts, but in each case the stridulation noise consists of a regular succession of pairs of pulses of high frequency sound. There is a short interval between the pulses of a pair, and a comparatively long silent interval between the pairs. The oscillograms appear to be in accordance with the manner in which the sound is produced, i.e., by projections on the two back legs rubbing over the edges of the wing cases. Presumably each pair of pulses corresponds to an up-and-down motion of the back legs moving in approximate synchronism, and the high-frequency components of the pulses are associated with natural frequencies of the wing cases. The pulses and intervals are approximately constant throughout a record, but they differ in detail from one record to another, e.g., record 2 shows a pronounced minimum in the first pulse, and the interval between the pulses is longer than in records 1 and 3.

The following table summarises the results obtained from a number of records :

TABLE I.

	Duration of first pulse (secs.).	Short interval (secs.).	Duration of second pulse (secs.).	Long interval after second pulse (secs.).	Time for complete cycle (secs.).
Range of values	0·010–0·016	0·001–0·012	0·010–0·028	0·051–0·068	0·085–0·107
Average value .	0·013	0·005	0·019	0·060	0·097

The second pulse is usually longer and more drawn out than the first pulse, and the whole cycle is repeated about 10 times per second.

Plate 2 gives three records taken at the faster speed, and showing in each case the detailed features of a pair of pulses. It may be noted that the records represent the combined effect of two sources of sound, one on each side of the insect, probably acting together and having somewhat different characteristics. The resultant wave forms appear to be too complex for an exact mathematical analysis, but approximate measurements show that the most prominent frequency is usually of the order of 13,000 c.p.s., both for the first and second

pulses, various records giving values ranging from about 12,000 to 15,000 c.p.s. Components of the order of 8000 c.p.s. can also be detected among the other frequencies present. The records do not give a clear indication of regular amplitude modulation within the main pulses, but it may be observed that pronounced fluctuations occur having periods of the order of 0·001 sec.

(b) *Analysis.*

Fig. 1 shows the acoustic spectrum of a stridulation, as given on the screen of the analyser. Each spot or line corresponds to a one-third octave frequency
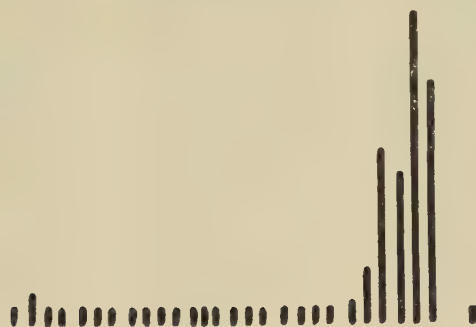
Fig. 1.—Sound spectrum of stridulation noise.

band, and the mean frequencies of the bands, read from left to right, are given in the following table :

TABLE II.

No. of band.	Mean frequency (c.p.s.).	No. of band.	Mean frequency (c.p.s.).	No. of band.	Mean frequency (c.p.s.).
1	40	10	320	19	2500
2	50	11	400	20	3200
3	64	12	500	21	4000
4	80	13	640	22	5000
5	100	14	800	23	6400
6	125	15	1000	24	8000
7	160	16	1250	25	10,000
8	200	17	1600	26	12,500
9	250	18	2000	27	16,000

The 28th spot, on the extreme right, was not used.

In the figure, which is typical of the results obtained, the components shown are confined to bands 22–27, having mean frequencies from 5000 to 16,000 c.p.s. and the greatest intensity is in band 26, with a mean frequency of 12,500 c.p.s. The line shown in band 2 (50 c.p.s.) is due to mains interference and does not represent a component of the locust noise. It should be noted that the intensity range of the analyser was about 20 decibels ; i.e., components more than 20 decibels below the largest component shown in the photograph would not be detected. Also the upper cut-off frequency of the highest band

of the analyser was about 18,000 c.p.s., and there may be higher frequencies than this present in the stridulation noise.

The following table gives the results of a number of analyses. The intensities are expressed in terms of decibels above an arbitrary zero.
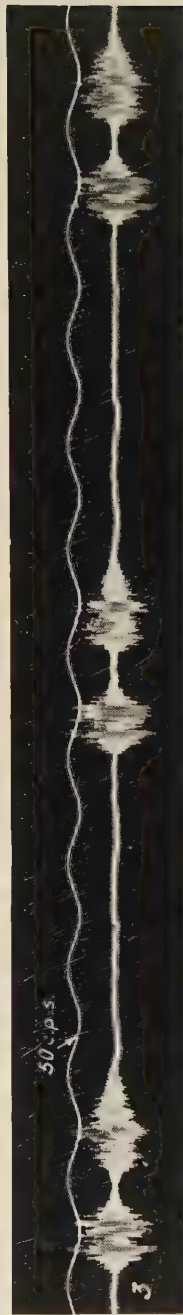
TABLE III.

Record.	Relative intensity (decibels) in one-third octave band of mean frequency (c.p.s.).					
	5000.	6400.	8000.	10,000.	12,500.	16,000.
a	1	3	12	12	19	16
b	.	0	6	5	16	7
c	.	0	8	9	15	18
d	1	4	14	13	19	17
e	2	6	11	9	17	11
f	.	3	10	10	16	7
Average	.	3	10	10	17	13

In one case the intensity is greatest in the highest frequency band, but in the others the maximum occurs in the 12,500 c.p.s. band and there is a tendency to a subsidiary maximum in the region of 8000 c.p.s. These results are in general agreement with those obtained from the oscillograph records.

ACKNOWLEDGMENTS.

Plate 1.
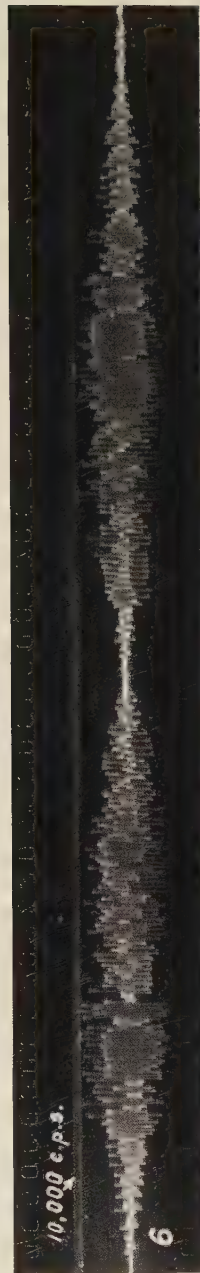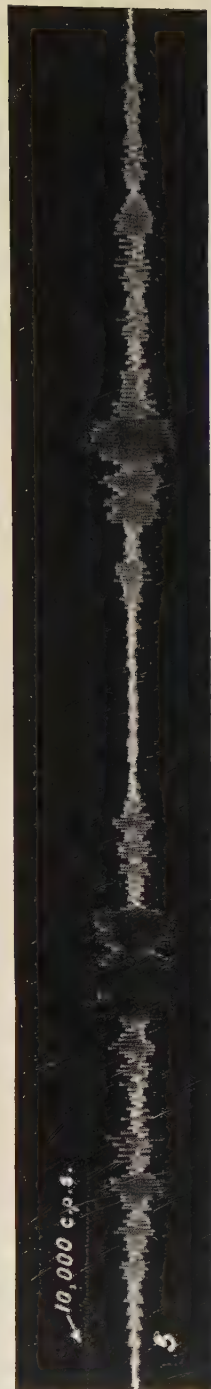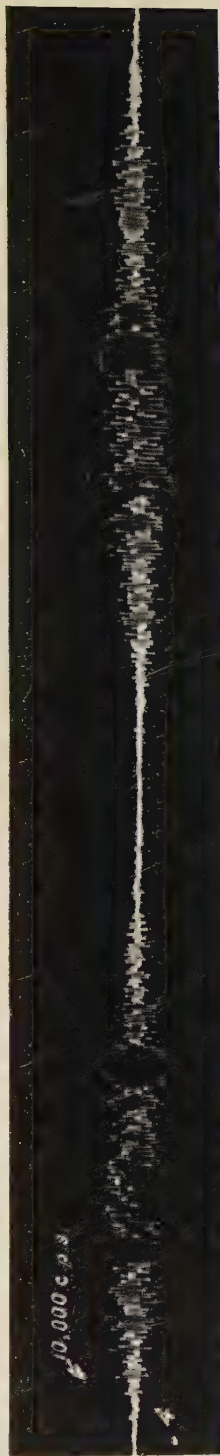

Oscillograms of stridulation noise.   Time scale 50 c.p.s.

E. J. Evans.

Plate 2.

Oscillograms of stridulation noise.   Time scale 10,000 c.p.s.

E. J. Evans.

Adlard & Son, Ltd., Dorking.

THE PUPA OF *ISOPOGON BREVIROSTRIS* MEIGEN (DIPTERA, ASILIDAE).

By L. Parmenter, F.R.E.S.

Turning over a stone on 22nd May, 1950, near Alfriston, Sussex, Mr. E. E. Syms found an Asilid pupa in the earth in a vertical position. Under the same stone was a small nest of a black ant, probably *Lasius niger* L. The fly, *Isopogon brevirostris* Meigen, a male, emerged on 31st May, 1950.

I am indebted to Mr. E. E. Syms for lending me the specimen to study and to Mr. C. O. Hammond for preparing the drawings.

This species was not studied by Melin who, however, described the pupae of 15 species of Asilidae that have been found in this country. His work remains the basis of our knowledge of the early stages of the European species of this family.

Dried pupal pelt yellow, 10 mm. in length and 3 mm. in width at its widest part.

Head with a pair of broad-based anterior antennal horns with dark brown pointed tips and with a short fine bristle at base behind each horn. Each of the pair of posterior processes with tooth, blunter and shorter than the anterior horn and another blunt tooth closely joined to a broader flange, creased diagonally at the base. Whole process brown with blackish tips to teeth and flange, the latter representing the third tooth as found in all the other Asilid pupae described by Melin.

A pair of sheaths protrude from under main facial sheath, on either side of heart-shaped open area, the tips just extending over the first leg sheath. No bristles on the face.

Thorax similar to other Dasypogoninae pupae.

A projecting prothoracic spiracle (fig. 7) and two pointed dark brown processes at base of second leg sheath. A line of small punctures crosses dorsum just below, but not reaching as far sideways as the two prothoracic spiracles.

Abdominal segments 1–7 with dark brown hooks with down-curved tips across the dorsum. At junction between tergites and sternites on each segment is a spiracle with a few (3–6) yellow bristles below, level with the dorsal hooks or spines. These hooks strongest on segment 1 and more curved than on other segments. Spines at each end of the row of 13 are thinner and more curved.

Segment 2 ringed one-third from the base with straighter hooks. In centre line a short bifid process with three long spines on either side. Alternately between these are short straighter spines with three very small ones at the outer edge followed by a yellow bristle (not shown in fig. 4).

Segment 3 similar with the ring half-way from the base and several yellow bristles extending the ring towards the side.

Segment 4 with two short spines centrally followed by three pairs of alternate long and short spines and, in turn, by the yellow bristles.

Segments 5 and 6 similar but with only a single short spine in centre of ring in place of the pair on segment 4 and the bifid spine on segments 2 and 3.

Segment 7 with six long hooks with only two tiny stumps in place of the alternate short spines of previous segments. Many long yellow bristles extend the ring on either side to the side margins.

Segment 8 with four long brown hooks with an abundance of long yellow bristles encircling entire abdomen. Segments 6 and 7 with a few yellow bristles on each side of ventral surface.

Apical portion of abdomen with two pairs of terminal processes, each pair consisting of two long brown-black sharp-pointed spines with two short spines between. Posterior spine longer than anterior, which bears a fine-pointed branch in one case. Fig. 8 shows the two pairs differing in the single specimen examined.

REFERENCE.

MELIN, D., 1923, Contributions to the knowledge of the biology, metamorphosis and distribution of the Swedish Asilids in relation to the whole family of Asilids.   *Zool. Bidr. Uppsala* **8** : 1–317.
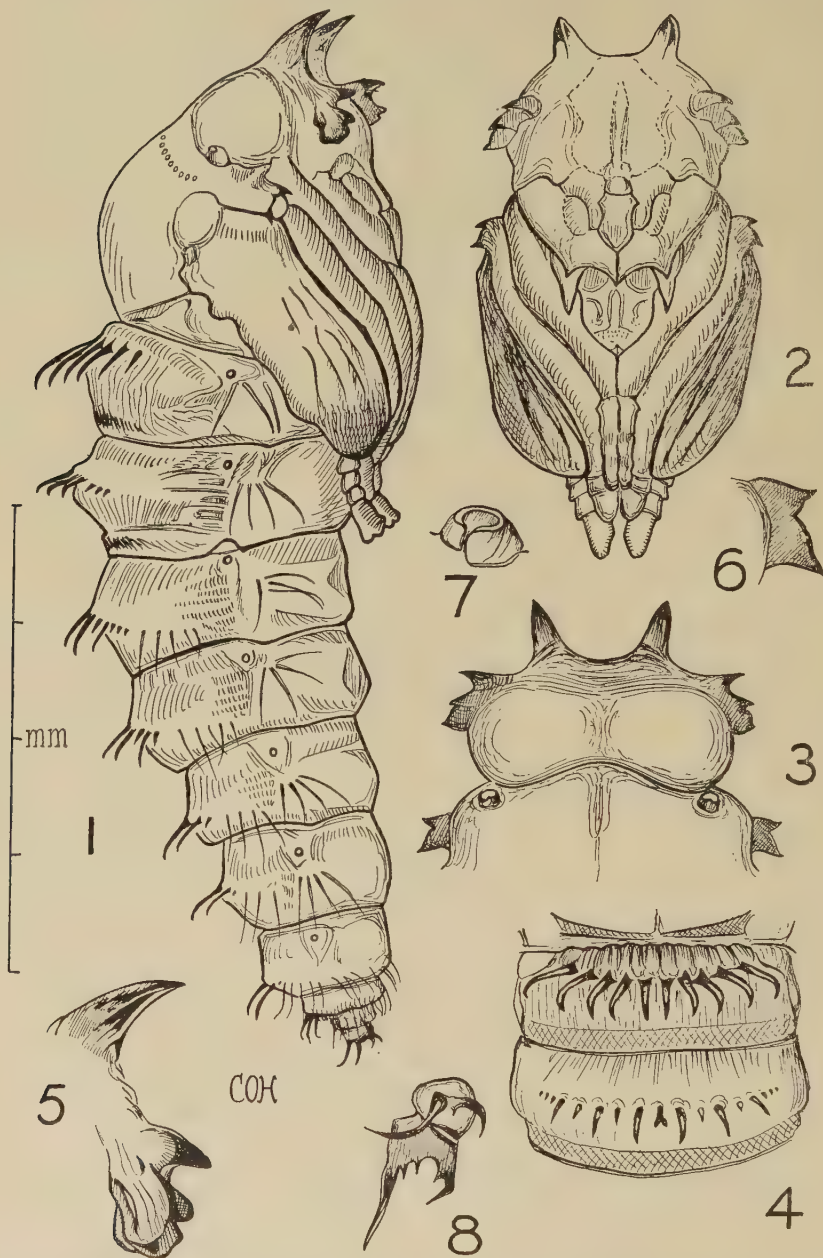
FIGS. 1–8.—*Isopogon brevirostris* Mg. (1) Pupa, side view ;   (2) ventral view, head and thorax ;   (3) dorsal view, head and upper thorax ;   (4) segments 1–2 of abdomen, dorsal view ;   (5) antennal processes ;   (6) process at the base of second pair of legs ; (7) prothoracic spiracle ;   (8) apical spines of abdomen.

(Figs. 1–4 to scale shown.   Figs. 5–8 further enlarged.)

AN ANALYSIS OF CAPTURES OF HEMEROBIIDAE AND CHRYSOPIDAE IN SUCTION TRAPS AT ROTHAMSTED, JULY, 1949.

By C. J. Banks, B.Sc.

(*Dept. of Entomology, Rothamsted Experimental Station, Harpenden.*)

The following work forms part of a study of the populations and activity of the predators of the Black Bean aphid, *Aphis fabae* (Scopoli). Hemerobiidae and Chrysopidae are important predators of the pest, both as larvae and as adults. The present work describes the results of continuous day and night sampling by suction traps over two crops, beans and potatoes, from 5th July to 2nd August, 1949, and relates to the numbers of adult Neuroptera captured. There are no records for previous months for comparison, so that little may be said about the population trend during that year.

METHODS.

Two suction traps were set up in the crops, Trap A over a plot of beans, and Trap B over a plot of potatoes, for the purpose of sampling aphids flying over the crops. The traps, which automatically separate the catches into hourly lots, have been described in detail by Johnson (1950). Each trap was 9 in. in diameter, and was set up vertically in the centre of the crop with its mouth at approximately crop level (Trap A 4 ft. 6 in., Trap B 3 ft. 6 in. above ground). Trap A (beans) was in a sheltered garden at Rothamsted Lodge, and Trap B (potatoes) was in a more exposed site near the Main Laboratory about $\frac{1}{4}$ mile away ; on one side of the potato plot was a plot of sugar beet, and on the other a plot of beans. Each trap samples approximately 19,000 cu. ft. of air per hr. (Johnson, 1950).

The following records of the physical environment of the crops were made :

(*a*) *Temperature* was recorded on a thermograph placed in an unventilated Stevenson screen 2 ft. above the ground near Trap A ; the mean temperature for each hour of the day and night was obtained from the readings.

(*b*) *Wind speed* was recorded on a revolving drum by a sensitive Casella anemometer.

(*c*) *Rainfall* and *relative humidity* data were obtained from the regular records of the Meteorological Section of the Laboratory, taken about 100 yards away from Trap B.

All temperatures are given in °C. and all times as Greenwich mean time.

Sunset over the period was from 20.20 hr. to 19.51 hr. ; sunrise was from 03.47 hr. to 04.21 hr.

ANALYSIS OF THE CATCHES.

All the Neuroptera were caught at night and none during the day-time, although most days were calm with wind speeds less than 3 m.p.h. The following species were captured :

Trap A (Beans) : —   Total captured.

    Family HEMEROBIIDAE :

        Kimminsia subnebulosa (Stephens) .   .   .   113

        Hemerobius humulinus Linnaeus   .   .   .   14

    Family CHRYSOPIDAE :

        Chrysopa carnea Stephens   2

Trap B (Potatoes) :—

    Family HEMEROBIIDAE :

        Kimminsia subnebulosa (Stephens) .   .   .   16

        Eumicromus angulatus (Stephens)   .   .   .   1

        Micromus variegatus (Fabricius)   .   .   .   1

    Family CHRYSOPIDAE :

        Chrysopa carnea Stephens   8

        C. albolineata Killington   1

        C. flavifrons Brauer   1

        C. septempunctata Wesmael   1

Trap A (Tables I, II, fig. 1).—Only 2 *Chrysopa* were captured during the period of 29 nights. Hemerobiidae occurred on nearly all nights and were of

TABLE I.—*Captures of Neuroptera, Trap A.*

Date : July—	K. subnebulosa.			H. humulinus.			Total HEMEROBIIDAE.			Total CHRYSOPIDAE.
	♂.	♀.	Total.	♂.	♀.	Total.	♂.	♀.	Total.	
5–	1	.	1	.	.	.	1	.	1	.
6–	1	.	1	.	.	.	1	.	1	.
7–	1	.	1	.	.	.	1	.	1	.
8–	1	.	1	.	.	.	1	.	1	.
9–	3	.	3	.	.	.	3	.	3	.
10–	2	.	2	.	.	.	2	.	2	.
11–	3	.	3	.	.	.	3	.	3	.
12–	1	.	1	.	.	.	1	.	1	.
13–	9	4	13	1	.	1	10	4	14	.
14–	.	.	.	.	.	.	.	.	.	.
15–	4	2	6	.	.	.	4	2	6	.
16–	2	2	4	.	.	.	2	2	4	.
17–	.	.	.	.	.	.	.	.	.	.
18–	4	.	4	.	.	.	4	.	4	.
19–	3	.	3	.	.	.	3	.	3	.
20–	9	2	11	2	.	2	11	2	13	.
21–	8	.	8	1	1	2	9	1	10	.
22–	12	.	12	2	.	2	14	.	14	.
23–	15	2	17	1	2	3	16	4	20	.
24–	5	2	7	1	.	1	6	2	8	.
25–	6	1	7	1	.	1	7	1	8	.
26–	5	.	5	1	.	1	6	.	6	1
27–	1	1	2	.	.	.	1	1	2	.
28–	.	1	1	.	1	1	.	2	2	1
Totals	96	17	113	10	4	14	106	21	127	2

two species only, *K. subnebulosa* and *H. humulinus*, the former being more numerous ; the males of both species far outnumbered females. The largest numbers of *K. subnebulosa* and *H. humulinus* occurred on 13th, 20th, 21st, 22nd and 23rd July. On two nights, 14th and 17th July, no Neuroptera were captured.
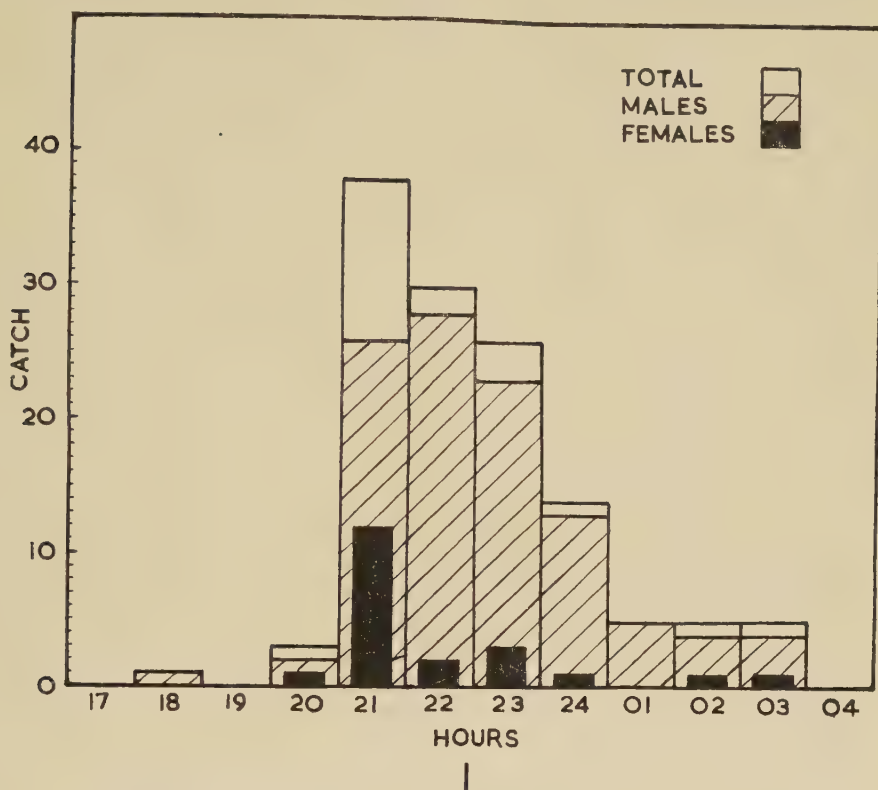

Fig. 1.—Times of capture of Hemerobiidae, Trap A.

Table II.—*Total hourly catches of* Hemerobiidae, *Trap A.*

Time.	K. subnebulosa.			H. humulinus.			Total Hemerobiidae.		
	♂.	♀.	Total.	♂.	♀.	Total.	♂.	♀.	Total.
18.00–	1	.	1	.	.	.	1	.	1
19.00–	.	.	.	.	.	.	.	.	.
20.00–	2	.	2	.	1	1	2	1	3
21.00–	24	11	35	2	1	3	26	12	38
22.00–	28	2	30	.	.	.	28	2	30
23.00–	20	2	22	3	1	4	23	3	26
24.00–	8	1	9	5	.	5	13	1	14
01.00–	5	.	5	.	.	.	5	.	5
02.00–	4	.	4	.	1	1	4	1	5
03.00–	4	1	5	.	.	.	4	1	5
Totals . .	96	17	113	10	4	14	106	21	127

The largest numbers of Hemerobiidae were captured between 21.00–01.00 hr., with a maximum between 21.00–22.00 hr. (Table II, fig. 1). Only one specimen of *K. subnebulosa* was caught before 20.00 hr. and none after 04.00 hr. No conclusions may be drawn from the Chrysopidae.

Trap B (Tables III, IV).—The total number of all species captured in the more exposed Trap B was much lower than in Trap A, but there was a greater

TABLE III.—*Captures of Neuroptera, Trap B.*

Date : July—	HEMEROBIIDAE.			CHRYSOPIDAE.		
	♂.	♀.	Total.	♂.	♀.	Total.
5–	1	.	1	.	.	.
6–	.	.	.	.	.	.
7–	.	.	.	.	.	.
8–	.	.	.	.	.	.
9–	.	.	.	.	.	.
10–	.	1	1	.	.	.
11–	1	1	2	.	1	1
12–	.	.	.	.	.	.
13–	.	.	.	.	1	1
14–	.	.	.	.	1	1
15–	1	1	2	.	.	.
16–	.	.	.	.	1	1
17–	1	.	1	.	.	.
18–	.	.	.	.	.	.
19–	.	.	.	.	.	.
20–	.	.	.	.	.	.
21–	1	.	1	.	.	.
22–	4	.	4	.	2	2
23–	.	1	1	1	2	3
24–	.	2	2	.	.	.
25–	.	1	1	.	.	.
26–	.	.	.	1	.	1
27–	1	.	1	.	.	.
28–	.	.	.	.	.	.
29–	1	.	1	1	.	1
30–	.	.	.	.	.	.
31–	.	.	.	.	.	.
Aug.—						
1–	.	.	.	.	.	.
2–	.	.	.	1	.	1
Totals	11	7	18	3	8	11

diversity of species of both families (3 spp. in A, 7 in B), and the Chrysopidae were more numerous. The maximum numbers of Neuroptera occurred on the nights 22nd–24th July, as with Trap A. Among the Hemerobiidae the males were only slightly more numerous than the females, but the total number caught is too small to allow any definite conclusions to be drawn. Female Chrysopidae were more numerous than the males.

The maximum catch of Hemerobiidae was between 24.00–01.00 hr., and of Chrysopidae between 21.00–23.00 hr. (Table IV). No Hemerobiidae were obtained before 20.00 hr. or after 04.00 hr., and Chrysopidae captures occurred between 21.00–03.00 hr.

TABLE IV.—*Total hourly catches of Neuroptera, and list of species captured.*
Trap B.

Time.	HEMEROBIIDAE.			CHRYSOPIDAE.		
	♂.	♀.	Total.	♂.	♀.	Total.
18.00–	.	.	.	.	.	.
19.00–	.	.	.	.	.	.
20.00–	.	.	.	.	.	.
21.00–	2	2	4	2	.	2
22.00–	.	.	.	1	3	4
23.00–	1	1	2	.	3	3
24.00–	3	2	5	.	.	.
01.00–	1	1	2	.	1	1
02.00–	2	1	3	.	1	1
03.00–	2	.	2	.	.	.
Totals	11	7	18	3	8	11

	HEMEROBIIDAE.					CHRYSOPIDAE.		
	♂.	♀.	Total.			♂.	♀.	Total.
K. subnebulosa .	10	6	16	*C. carnea* .	.	3	5	8
E. angulatus .	.	1	1	*C. albolineata* .	.	.	1	1
M. variegatus .	1	.	1	*C. flavifrons* .	.	.	1	1
				C. septempunctata .	.	.	1	1
Totals . . .	11	7	18					
				Totals . . .		3	8	11

The results for the two traps indicate that the period of maximum activity for the Hemerobiidae is between 21.00–23.00 hr., with a peak at 21.00–22.00 hr., the hour of dusk, while the Chrysopidae seem to be more active between 21.00–23.00 hr. Williams and Killington (1935), using a light trap at Rothamsted, found that Hemerobiidae were captured earlier (before midnight) than Chrysopidae (after midnight).

The preponderance of males over females among the Hemerobiidae may possibly be due to the greater activity of the males, since Williams and Killington showed that in extensive breeding experiments approximately equal numbers of both sexes were obtained. The figures available for the Chrysopidae allow no definite conclusion to be drawn but suggest a greater activity by the females.

METEOROLOGICAL CONDITIONS AND THE CATCH.

Only the capture of Hemerobiidae in Trap A will be considered as figures for the other catches are too low.

Temperature.—Attempts have been made to find an association between the catch and the temperature of the atmosphere. As will be seen from fig. 2, which shows the total catch for the period with temperatures, there is a rise and fall in the catch which corresponds broadly with the rise and fall in the temperature. There are two main peaks in the catch, one on 13th–14th July, and the other on 23rd and 24th July, with a period of relatively low catch between them. There is no statistically significant difference between the mean temperature of capture and the mean temperature of the night (18.00–05.00 hr.).

The association which exists between catch and temperature may be shown in a number of ways, but is best expressed by using the log (catch + 1) rather than the actual numbers (Williams, 1937, 1940) and by calculating the coefficients of correlation (r) and regression (b) of the log catch on temperature.
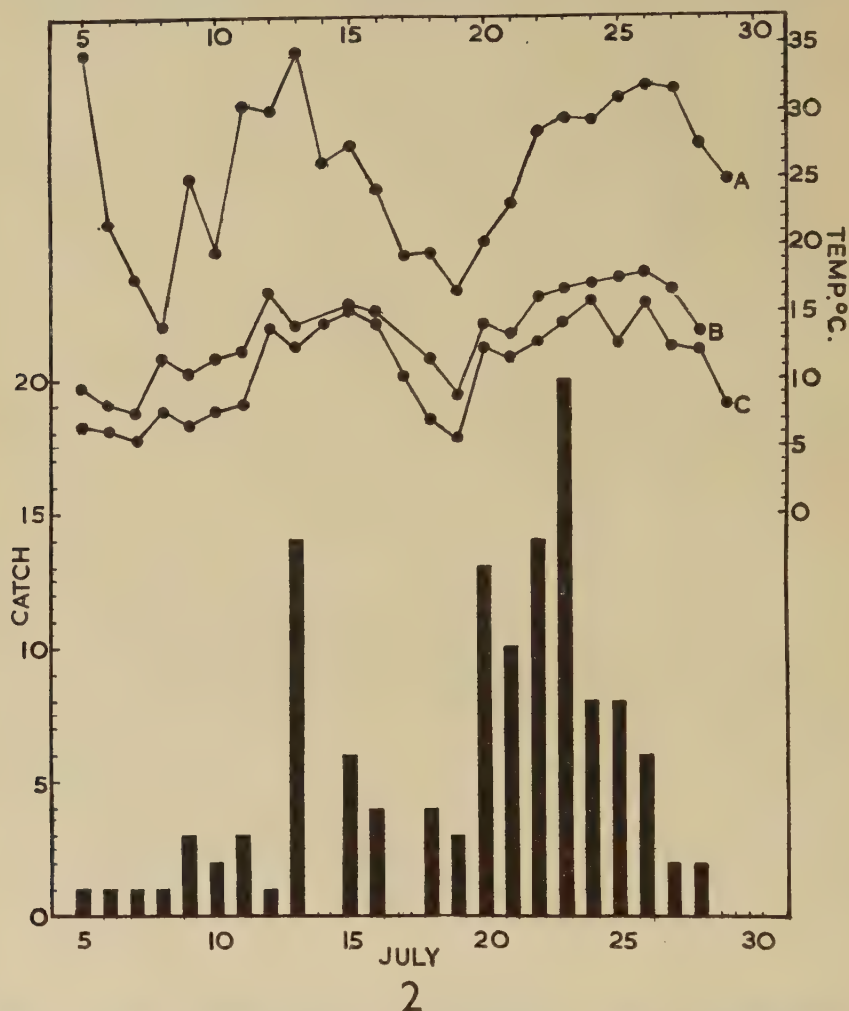

Fig. 2.—Captures of Hemerobiidae, Trap A, 5th–30th July, 1949, and temperatures for the period (A—maximum temp. of day preceding capture ; B—mean temp. of capture ; C—minimum temp. of night of capture).

Table V gives a number of such values of r and b. Significant values were obtained only for the actual temperature of time of capture and for the minimum temperature of the night.

Such correlation of catch and temperature would include two effects : changes in population over a long period and changes in flight activity over a relatively short period, dependent upon the local conditions at the time.

TABLE V.—*Coefficients of Correlation* (r) *and Regression* (b) *for Temperature and Log Catch.*

Temperature.					r.	b.	Remarks.
Actual temp. of capture	.	.	.	.	0·35	0·030	Significant.
Mean temp. of capture	.	.	.	.	0·35	0·043	Not significant.
Min. temp. of night	.	.	.	.	0·45	0·051	Significant.
Max. temp. of night (20.00–21.00 hr.)	.	.	.	0·16	0·058	Not significant.
Max. temp. of day before capture	.	.	.	0·30	0·020	,, ,,

To distinguish flight activity changes from the changes in population, *differences* between corresponding temperatures on successive days and the *differences* between corresponding log catch have been considered, including differences within the following temperatures : maximum and mean temperatures of the day of catch and of night of catch, minimum temperature of the night of catch, 5-day running mean temperatures, and maximum temperature of the day preceding the catch. Only in the last case was there any significant correlation. For example, the maximum temperature of 21st July (at 15.30 hr.) influenced the catch on the night of 22nd July ; the rise in maximum temperature from 23·05° on 21st July to 28·60° on 22nd July was accompanied by a rise in log catch from 1·04 on 21st July to 1·18 on 22nd July. Table VI and fig. 3

TABLE VI.—*Difference in maximum temperature of the day preceding the catch and corresponding differences in log catch.*

Date : July—	Max. temp. day before catch.	Differences in max. temp. Δt. +.	Differences in max. temp. Δt. −.	log (catch + 1).	Differences in (log catch + 1). Δc. +.	Differences in (log catch + 1). Δc. −.
4	32·15			0		
		2·20			0·30	
5	34·40			0·30		
			13·00		0	
6	21·40			0·30		
			3·80		0	
7	17·60			0·30		
			3·75		0	
8	13·85			0·30		
		11·15			0·30	
9	25·00			0·60		
			5·45			0·12
10	19·55			0·48		
		10·90			0·12	
11	30·45			0·60		
			0·55			0·30
12	29·90			0·30		
		4·60			0·88	
13	34·50			1·18		
			8·35			1·18
14	26·15			0		
		1·40			0·85	
15	27·55			0·85		
			3·30			0·15
16	24·25			0·70		
			5·00			0·70
17	19·25			0		
		0·35			0·70	
18	19·60			0·70		
			2·95			0·10
19	16·65			0·60		
		3·60			0·55	
20	20·25			1·15		
		2·80				0·11
21	23·05			1·04		
		5·55			0·14	
22	28·60			1·18		
		0·90			0·14	
23	29·50			1·32		
			0·15			0·37
24	29·35			0·95		
		2·70			0	
25	31·05			0·95		
		0·75				0·10
26	31·80			0·85		
			0·10			0·37
27	31·70			0·48		
			4·20		0	
28	27·50			0·48		
			2·65			0·48
29	24·85			0		
			1·55		0	
30	23·30			0		

show the relation between the differences of log catch (Δc) and differences between successive maximum temperatures of the day preceding the catch (Δt). The correlation coefficient was 0·46 and the regression of Δt on Δc was 0·039.
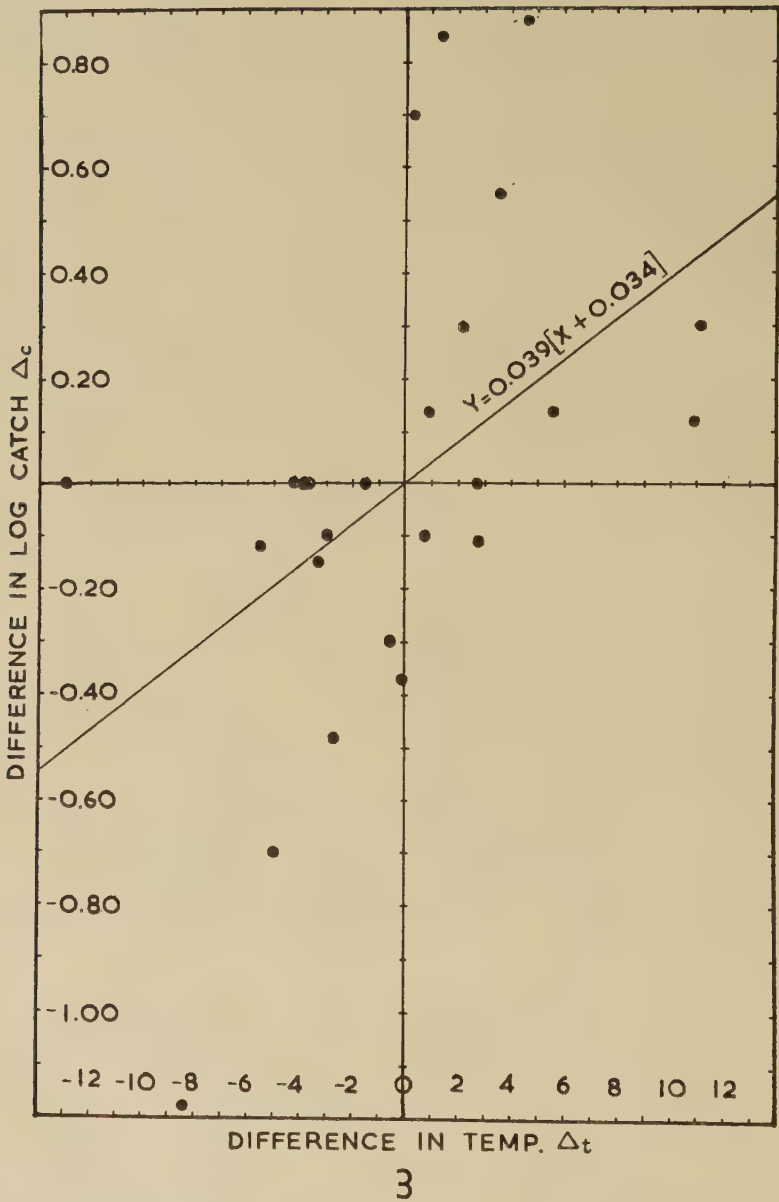

FIG. 3.—Scatter diagram and regression line showing the relation between difference in log catch (Δc) and difference in maximum temp. of the day preceding the catch (Δt).

The effects of previous temperature conditions on the catch could be explained by supposing that they affected the numbers of adult Neuroptera emerging the day before ; thus, even the night-to-night changes in catch cannot yet be considered as reflecting only changes in flight activity.

METEOROLOGICAL FACTORS OTHER THAN TEMPERATURE.

Wind speed.—Wind speed during the hours when insects were caught (18.00–05.00 hr.) varied from 0·80–1·17 m.p.h., with a mean at which captures were made of 0·85 m.p.h.   All wind speeds for the whole night were very low and never exceeded 2·30 m.p.h.   There were many occasions when the wind speed was at or lower than the mean yet no captures were made.   There seems to be no association between wind speed and catch or absence of catch in the present data, although there is no doubt a maximum wind speed above which various Neuroptera will not fly.

Rainfall.—No rain was recorded in June, 1949, and in July only negligible quantities were recorded, a total of 1·16 in.

Relative humidity.—The R.H. varied from 75·6–99·5 per cent. with a mean of 88·3 per cent. during the month.   There was no association between R.H. and catch.

ACKNOWLEDGMENTS.

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LABORATORY BREEDING OF *PIERIS BRASSICAE* L. AND *APANTELES GLOMERATUS* L.

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INTRODUCTION.

THE laboratory methods described in this paper were developed to give an all-the-year-round supply of *Pieris brassicae* L. and *Apanteles glomeratus* L. required in connection with experiments on systemic insecticides. The methods and equipment have yielded all the insects that could be desired throughout the winter and early spring of 1950–1951.

Pieris brassicae L.

Equipment.

The culture was established in a greenhouse maintained at about 20–25° C. and 50–70 per cent. R.H. The larval cages were wooden framed enclosures measuring 12 in. square at the base and 15 in. high. The top and back were muslin and the other sides glass. The front was divided in half horizontally. Each glass half slid in a groove at the bottom, but at the top was held in position by twist buttons. It could thus be lifted off when the larvae pupated on the glass. Doors which only slide are most unsatisfactory. As the work of Way, Hopkins and Smith (1949) had shown that diapause could be broken by extending the day length during the larval period to about 16 hours, fluorescent lamps were arranged over the cages. The light intensity is not critical and need not be more than a few foot candles. It is unwise to overcrowd or neglect to clean out or feed the larva as they are then likely to become diseased.

Some difficulty was experienced in getting the adults to mate in a small cage, and the one finally utilized measured 40 × 30 × 36 in. high. It had glass walls except on the top and half of one long side which were covered with muslin. The side curtain was found to be much more convenient than a door. Over this cage a fluorescent lamp extended the day length to 16 hours, and there was also a 500 wt. tungsten filament lamp in an enamelled reflector which was used to give a sunlight effect for 6 hours ; without this latter lamp the adults were disinclined to fly, feed or oviposit on dull days. Inside the cage there were 2–3 small cabbage plants on which the adults oviposited, and about 6–8 artificial flowers on long glass rod stalks which stuck in a large pot of sand and held the " flowers " within about 6–8 in. of the top of the cage about 12 in. directly below the tungsten lamp. The artificial flowers were made from pieces of glass tube about $2\frac{1}{2}$ in. long and 0·25 in. in internal diameter. Each was sealed across the middle so as to give a cup at one end which held about 1 c.c. of 7·5 per cent. honey solution and a cap at the other to slip over the top of the glass rod stalk. This allowed the " flowers " to be removed for cleaning. Around the top of the cup was a paper corolla about $\frac{1}{4}$–$\frac{1}{2}$ in. wide (fig. 1). The paper was stained dark blue with an aqueous solution of aniline blue, since it has been shown that *Pieris brassicae* L. spontaneously selects blue and purple flowers in preference to others (Ilse, 1928).

Breeding Technique.

The culture was started from eggs collected in the field, since experience had shown that they were less frequently parasitized than larvae. It could equally well be started with adults. Patches of leaves bearing eggs were placed on small potted cabbage plants in the larval cages. In the later instars the large amount of food necessary was given as cut cabbage or other similar leaves. The full-grown larvae pupated in these cages and later gave rise to adults which were transferred to the adult cage. Here they fed and mated and later oviposited on the potted cabbage plants provided. These were changed daily so that eggs of known age were available.
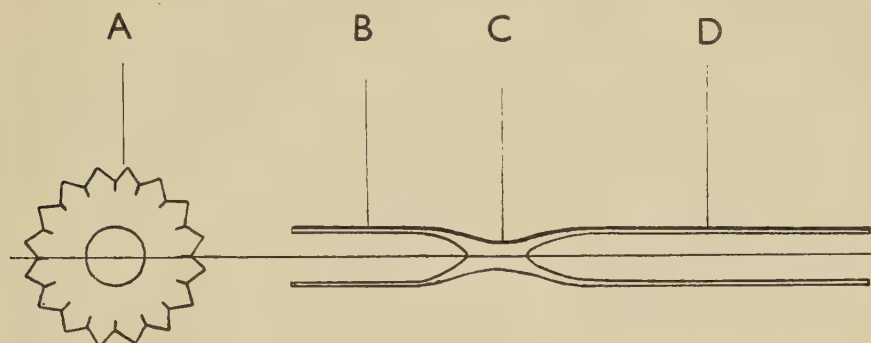
FIG. 1.—The artificial flowers on which the adults fed. A, the blue paper corolla ; B, the tube for the honey solution ; C, the seal ; D, the cap which fits over the glass-rod stalk.

TABLE I.—*A comparison between laboratory bred* Pieris brassicae *L. and wild specimens. The data for the latter are from Frohawk, 1934.*

Stage.	Laboratory bred insects.		Wild insects.
Eggs :			
Number per batch	55	.	.
Days to hatch	6	.	8–10
Percentage hatching . . .	100	.	.
Larva :			
Days to feed	16–24	.	30
Length full grown (mm.) . . .	40	.	41
Pupae :			
Duration of pupal period . . .	17–30	.	14
Length (mm.)	25	.	25·4
Adult :			
Length of life (days)	5–13 majority others up to 34	.	25
Wing span (mm.)	53♂, 58♀	.	63♂, 76♀

The insects bred in the way described resembled wild insects (Frohawk, 1934), except that the adults usually lived for a shorter period than wild specimens.   This was probably due to the overcrowded conditions and inadequate supply of artificial flowers in the adult cage.   They were also smaller as judged by wing span than those measured by Frohawk, but compared favourably with the local spring brood, which had wing spans of 56 mm. ♂ and 56 mm. ♀.

It was of interest to see that even the large larvae did not eat the patches of eggs on cabbage leaves.   They often nibbled to the very edge of the egg patch on all sides and detached it from the leaf, but there was never any evidence that the marginal eggs were damaged.   These isolated patches of eggs hatched normally in the cases examined.

Apanteles glomeratus L.

Equipment.

The equipment used in breeding the *Apanteles* was the same as that used for *Pieris*, and included the light equipment, which extended the day to 16 hours. The insects were housed in the greenhouse or in a constant temperature room maintained at 20° C. and 70 per cent. R.H.

Breeding Technique.

Apanteles glomeratus L. lays its eggs in the newly hatched larvae of *Pieris* and chooses almost exclusively those not more than 2–3 days old (Picard, 1922 ; Moss, 1933).

The young cabbage plants on which the caged *Pieris* adults had oviposited were placed in a cage containing *Apanteles*.   The relative numbers of larvae and parasites were adjusted to obtain a high level of parasitism.   When making this adjustment it was necessary to obtain an indication of the sex ratio of the parasites as this rather frequently departed from 50 : 50, some cultures being almost exclusively male.   The parasitized larvae were then fed in the normal way.   As the caterpillar prepared to pupate the *Apanteles* larvae bored their way out and spun their characteristic yellow cocoons.   The adults emerged about 15–20 days later at about the same time as any unparasitized *Pieris* appeared.   The adults fed readily on dabs of honey placed on the walls of the cage and they were also given wet cotton-wool ; alternatively a honey-water mixture may be provided.   To prolong the life of the adults they should be kept in a cool dark room.   They were capable of ovipositing soon after emergence.

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OBSERVATIONS ON THE CAPACITY FOR FLIGHT OF WATER BEETLES.

By Dorothy J. Jackson, F.R.E.S., F.L.S.

In autumn, 1949, I collected a number of *Noterus capricornis* Herbst in Kilconquhar Loch, Fife, and, on dissecting some of the specimens, I found that, though the wings were fully formed, the muscles of flight were absent (1950). There could be no doubt that, at the time of dissection, these beetles were incapable of flight. I found *N. clavicornis* Deg. to be abundant in another loch in Fife—Lindores Loch—and I took many specimens when I visited it in May, 1949, and again in March, 1951. All the specimens examined—50—had brachypterous wings. From other localities specimens of *N. clavicornis* have been seen with larger but not full sized wings. Partially reduced wings have also been found in examples of *Agabus undulatus* Schr. from Askham Bog, Yorkshire, and no flight muscles were present in the beetles dissected.

A few other species of water beetles are known to be brachypterous. In *Agabus maderensis* Woll., Professor F. Balfour-Browne (1950) found both fully developed and shortened wings, and the same has been observed by Leech (1942) for *Agabus bifarius* Kirby. Leech also refers in this paper to other records ; completely apterous species of the Dytiscid genus *Siettita* from deep wells in France, and a new genus of Hydrophilid described by J. Balfour-Browne (1939) from Lake Tanganyika in which the wings are reduced to mere functionless slips. Sharp (1916) records abbreviated wings for one species of aquatic *Helophorus*, *H. granularis* L. (= *ytenensis* Sharp), in which the form he considered to be a different species, *ytenensis*, differed from the type principally in having abbreviated wings. Professor Balfour-Browne has recently informed me that he has found specimens of *Hydraena minutissima* Steph. to be brachypterous, and one specimen of *H. pygmaea* Waterhouse which he examined had apparently no wings.

These records show that the capacity for flight is not essential for all species of water beetles, but how far ability to fly is of importance to the survival of a species will depend largely upon the habits of the species and the sort of habitat it frequents. To the species frequenting temporary waters it seems obvious that flight must be an advantage, though it is interesting to find that Leech took *Agabus bifarius*, with reduced wings, in ephemeral ponds, and he believed that the adults aestivated below the surface of the soil, or possibly in decaying water-soaked logs.

Species capable of flight will doubtless migrate sooner or later during periods of drought to other waters[1] but flightless species will probably burrow in the

[1] Professor Balfour-Browne (1906) considers that the beetle fauna does not disperse on the drying up of a pond or dyke, but remains somewhere in the vicinity, probably in cracks in the mud or amongst damp herbage at the sides. In the dry summer of 1949 I found in early June several specimens of *Agabus bipustulatus* L., a good flying species, under logs in dried-up cart ruts on rough ground, though a few small pools with sphagnum still held some water and were within easy reach. In October of the same year I visited a quarry pond in which the water had dried up, and on turning over stones lying on the cracked mud I found 23 *A. bipustulatus*. None of them were soft, so that they were not quite newly emerged. These observations show that even a strong flying species does not immediately migrate to water during drought. The stimulus to flight may depend on some physiological condition, such as hunger, or it may be controlled by atmospheric conditions. More investigations on this point would be of interest.

mud or seek damp spots under stones and remain in such positions until the autumn rains. Water beetles are probably able to survive a considerable time out of water if in fairly damp surroundings, and Wesenberg-Lund (1912) believes that the imagines of Hydroporines, Agabines, *Colymbetes* and *Ilybius* live for a long time as land beetles. In an experiment with *Hydroporus palustris* L. I confined some beetles in glass cylinders stuck into a lawn in February and March, and the beetles were still alive six weeks later when the experiment was unavoidably interrupted. During all this time they had no access to water and lived amongst moss and grass on the surface of the soil.

Species finding the ideal living conditions in lakes will have no occasion to migrate, while those frequenting wet and boggy moorland will have little use for flight in normal seasons. It is probable that species well established in favourable surroundings will get on quite well without flying. In fact, loss of the power of flight may be an advantage to some species in preventing them from straying from an entirely suitable habitat. It is well known that some species occur only in a certain type of habitat and are even local there, while others are generally distributed, though not necessarily abundant. How far are these peculiarities correlated with the capacity for flight?

In the hope of throwing some light on these problems, investigations were started nearly two years ago with the object of finding out if incapacity for flight, due to the abnormal condition of the flight muscles, was common in water beetles, and, if so, whether the flightless condition occurred throughout the life of the individual, or whether after a short period of flight the muscles underwent degeneration. In text-books it is rare to find any mention of the flying capacity of a species—unless of the larger beetles—and it may have been too readily assumed that if a beetle had well-formed wings it must be able to fly. I have already examined over 1000 individuals of many species of Hydradephaga and some Hydrophilidae and the work is still in progress. I intend to publish a full account of this investigation when it is more complete, but in the meantime it is hoped that by bringing the facts already collected to the notice of those who are interested in water beetles, more information may be forthcoming.

Most of the species I have studied have been collected in Fife, but many interesting species have been sent me by Mr. E. S. Brown from English localities and by Dr. R. Richter from Morayshire. Other helpful material has come from Prof. Balfour-Browne, Mr. A. W. R. Bartindale, Dr. K. G. Blair, Mr. H. M. Russell, Mr. A. Smith and Mr. J. E. Marson. I am greatly indebted to Professor Balfour-Browne for his ready help with identification. All the species studied have, in the first instance, been sent to him to check my identification, and I have much appreciated his kindness in examining any specimen that has puzzled me—even after it has been more or less mutilated by dissection. I also wish to express my thanks to Miss E. Evans for the help she has so kindly given me in regard to the literature.

I have kept records of the condition of the reproductive organs of all the beetles dissected as a guide to the age of the beetle, for in the newly emerged beetle (easily recognised by its soft cuticle) the reproductive organs are extremely small, but they increase greatly in size during the life of the beetle. In the Dytiscidae studied the adult beetles would appear to live for about a year, emerging, in Fife, from July to September, but probably earlier in the south, as soft specimens have been sent me by Mr. E. S. Brown collected in early June

in Hertfordshire. In the late season last year soft specimens of various Dytiscidae were taken in Fife in October.

Results of Investigation

The results so far obtained from this investigation into the flying capacity of water beetles show that great variation exists in regard to the condition of development of the flight muscles in different species, and sometimes in nearly related species. In many species fully developed muscles of flight are present in all specimens examined at all times of the year, and many specimens have been seen to fly in tests which I have carried out. Some of the most ready fliers are *Hydroporous planus* Fab., *H. pubescens* Gyll., *Agabus bipustulatus* L., *A. nebulosus* Fab., *Ilybius fuliginosus* Fab., *Colymbetes fuscus* L., *Dytiscus marginalis* L., *Helophorus aquaticus* L., *H. brevipalpis* Bed. and *Hydrobius fuscipes* L. These species are all widely distributed and many of them are very common. In such beetles the flight muscles are enormously developed, filling up the metathorax, and they are immediately visible on dissection. The metatergum and the abdominal tergites are strongly sclerotic (excepting in *I. fuliginosus*, in which they are light coloured), and the discs of the pleural wing muscles, the basalar and the subalar discs, situated at the base of the wing, are very large and strong and usually darkly pigmented, though in the genera *Dytiscus* and *Ilybius* they may be partially transparent.

In other species the flight muscles have been abnormal or absent in all the specimens so far examined at all times of the year. In such specimens modifications occur in the structure of the metatergum, the prephragma and the postphragma are less developed and the discs of the pleural flight muscles are much smaller. In some species the metatergum is noticeably shorter than in the good flying species. The abdominal tergites—excepting those towards the apex of the abdomen—are frequently, but not always, feebly sclerotic in the flightless beetles. The histology of the abnormal flight muscles is entirely different from that of normal flight muscle, and is very like that which I have described (1933) in the flightless form of the weevil, *Sitona hispidulus* Fab. The slender, transparent muscle fibres are crowded with large elongated nuclei and there is no cross-striation, whereas in normal flight muscle the fibres are many times larger and the nuclei are very small and spaced further apart, and cross-striation is distinct.

The following species have so far been found only with imperfectly developed flight muscles or no flight muscles and with the discs of the pleural flight muscles small: *Deronectes assimilis* Payk., *D. elegans* Panz., *Oreodytes rivalis* Gyll., *Hydroporus ferrugineus* Steph.,[2] *H. morio* Aubé, *H. obscurus* Sturm, *Agabus guttatus* Payk. (in this species thinnish bundles of flight muscles have been found in some young specimens which are intermediate in development between normal and abnormal muscles), *A. labiatus* Brahm, *A. paludosus* Fab., *A. uliginosus* L. (from Dumfriesshire from Prof. Balfour-Browne), *Platambus maculatus* L.,

[2] Only four specimens of this rare beetle have been obtained, three sent me by Dr. Richter from Morayshire and one which I took in a spring near Longformacus, Berwickshire. No trace of flight muscles is present in any of them, and the modifications of the thorax all indicate incapacity for flight. Other probably flightless species are *Laccophilus hyalinus* Deg. and *Ilybius fenestratus* Fab., but only a few specimens of each (from Yorkshire) have been dissected.

Anacaena globulus Payk., *Hydraena nigrita* Germ. These species mostly frequent lochs, streams or moorland ponds, some are widely distributed and others local. In such flightless specimens the space that would have been occupied by the voluminous flight muscles is largely filled up with fat body and, in mature beetles, the anterior part of the ovaries and the accessory glands of the male reproductive organs are to be found extending into the metathorax.

In a third group of species the condition of the flight muscles has been found to be variable in different individuals; the discs also may be variable in size, and some individuals may be capable of flight but others are flightless.

In species which fly readily the flight muscles have been found in full development in beetles of all ages, only rarely showing slight signs of reduction in old specimens, and they are perfectly developed even in soft specimens. In species with abnormal flight muscles these have usually been found in the same condition in beetles of all ages, though in the older beetles they may be greatly obscured by fat body.

In the species in which the development of the flight muscles is variable the position is more puzzling; in some individuals the size of the discs is proportionate to the width of the muscle bundle; in others the discs are of normal size but the muscles are reduced. Specimens with normal and abnormal flight muscles have been found at all times of the year, but the results so far obtained indicate that a higher proportion of forms with perfect flight muscles are to be found amongst recently emerged beetles. This variable condition of the flight muscles in different individuals of a species has been found to be most common in Hydroporids, and has been specially studied in the common and widely distributed *H. palustris* L., of which over 100 specimens from various localities have been dissected. If it is assumed that well-formed discs are an indication that the flight muscles have originally been well developed, the results would suggest that some forms (those with abnormal flight muscles and small discs) are permanently flightless, but that others (with well-formed discs) have at first normally developed muscles which may sometimes persist until the beetle is quite old, but in other specimens they may degenerate much earlier.

Individuals with fully formed and others with reduced flight muscles have often been taken in the same locality, and at the same time, but in the case of *Oreodytes septentrionalis* Gyll. six specimens sent me by Dr. Richter from the Findhorn at Forres, collected on 1. viii. 1950, had perfect flight muscles, but those which I took in Loch Awe, on 20. ix. 1951, were incapable of flight, six being without trace of flight muscles and one showing only one or two small bundles.

The following species have been found with the condition of the flight muscles variable—perfect in some specimens, abnormal or reduced in others. The species marked with an asterisk are those in which one or more individuals have been seen to fly. *Deronectes duodecimpustulatus* Fab.,* *Oreodytes septentrionalis* Gyll., *Hydroporus discretus* Fairm.,* *H. erythrocephalus* L., *H. gyllenhalli* Schiödte,* *H. memnonius* Nic., *H. palustris* L.,* *H. striola* Gyll.,* *H. tristis* Payk., *H. longulus* Muls., *Agabus affinis* Payk., *Helophorus flavipes* Fab*. These species occur in a variety of habitats; some are widely distributed and others local.

It is probable that further research will show that an increasing number of species have to be assigned to the variable class. Thus, with *Noterus capricornis*

Herbst, 60 specimens have been dissected from Fife, Dumfries, Yorkshire, Cheshire, Norfolk, Suffolk, Oxfordshire, Middlesex and Surrey, and, with two exceptions, all have had abnormal flight muscles (or no flight muscles) and small discs. The two exceptions came from a pond on Hampstead Heath and were collected by E. S. Brown; one had perfect flight muscles and large discs, and the other normal but thin flight muscles and well-formed discs. Yet other specimens from the same pond were flightless. Similarly with *Agabus arcticus* Payk., 21 specimens have been dissected from Kinross, Elginshire, and the Orkney Islands, but only two (from the Orkneys) have had perfect flight muscles and large discs, 3 were intermediate, and in the rest flight muscles were abnormal or absent and the discs small. A contrasting case is that of *Agabus sturmi* Gyll. This species is usually to be found with perfect flight muscles, and several specimens have been seen to fly, but one or two have been taken with abnormal flight muscles and small discs. A very curious case is that of the common *Anacaena globulus* Payk. So far 53 specimens have been carefully dissected (mostly from Scotland), but no fibrous muscles of flight have been found in any, and the subalar and basalar discs are extremely small. Yet in an allied species, *A. limbata* F., out of 25 dissected, all but two have had perfect flight muscles and good-sized discs and two have been seen to fly. Perhaps such small species may be readily transported by birds or flying insects. Another species which should be included in the variable class is *Hygrotus inaequalis* Fab. Out of 34 dissected only 8 have had normal flight muscles, and four of these were seen to fly. *Hyphydrus ovatus* L. is an interesting species of peculiar shape, the short metatergum suggesting a feeble development of flight muscles. Out of 12 dissected (mainly from Yorkshire) only one had normal flight muscles. Though repeated tests have been made with many individuals not one has attempted to fly.

A species which appears to be intermediate between the flightless and the variable species is *Hydroporus umbrosus* Gyll. Fifteen specimens from Fife have been dissected and in some young specimens very thin flight muscles of normal histology have been found; in tests made some beetles have been seen to raise their elytra and one flew about half an inch, but in the majority no flight muscles at all could be found though in some the discs were well formed. It is probably a species capable only of feeble flight for a short period after emergence.

The flight muscles, if normally developed, are easily seen on dissection, but in beetles without obvious flight muscles very careful search has to be made for the abnormal flight muscles, and these, if found, have to be mounted and examined under a high power to see if the histology is really that of abnormal muscle, as sometimes the bundles supposed to be abnormal flight muscles have proved to be merely strands of tracheae surrounded with fat body.

In some of the apparently flightless species, such as *Platambus maculatus* and *Agabus labiatus*, which are very active runners, the muscles of the hind legs are greatly developed, filling up the lower part of the metathorax and looking superficially very like bundles of flight muscle, especially the muscles adjacent to the coxae which might be mistaken for the pleural wing muscles, but they are attached above to the anterior coxal fold and have no connection with the wing base. Their histology, moreover, is quite different from that of normal flight muscles, being of ordinary body muscle type, like the other leg muscles. A

study has been made of the metathorax and flight muscles of *Agabus bipustulatus*, and it is hoped to describe these fully in a later paper, with an account of the modifications occurring in the structure of the thorax and flight muscles in a flightless beetle.

Tests for Flight.

I have made experiments on the ability to fly of many species, and I have no doubt that all the species with perfect flight muscles are able to fly, if suitably stimulated. Sunshine in warm weather has been found to be the best stimulus, but they also fly in a warm room at night. The species to be tested were placed in a baking dish, the floor of which was lined with cardboard to afford the beetles a foothold, while the sides were sufficiently steep and slippery to prevent their climbing out. No beetles with abnormal flight muscles have been seen to fly. Such specimens, when placed in the testing dish, run about—often at great speed—seeking for a shady corner where they remain stationary for long periods, but if the dish is turned they again hurry to the shade. A beetle preparing for flight pauses with the forepart of the body slightly raised, the abdomen makes wriggling movements, protruding and withdrawing at the apex of the elytra, fluid is exuded from the anus, a split appears between the elytra and in a few moments the beetle takes to flight. The larger beetles can be heard to hum for a few moments before taking off. Some small beetles may fly suddenly, without any visible preliminaries. Sometimes beetles, when falling on their backs in their efforts to scale the side of the testing dish, open their elytra and spread their wings to help them to get right side up and, once up, the wings are usually immediately folded. This happens often with the flightless species of *Anacaena globulus*.

In the absence of the pleural wing muscles the spreading of the wings is evidently effected by the contraction of a small tubular muscle, probably homologous with the musculus coxo-dorsalis of Bauer (Korschelt, 1923 : 577), which, in *Anacaena*, arises from a narrow fold in the side of the scutum just above the wing base, and extends downwards to its insertion by a tendon in the coxa. By pressing this muscle inwards with a needle, or pulling it with forceps, the wing extends, The refolding of the wings will be initiated by the action of other small tubular muscles present at the wing base. It is only the fibrous muscles of flight that are absent. In *Agabus bipustulatus*, in which the flight muscles are fully developed, the musculus coxo-dorsalis is relatively smaller than in *Anacaena*, and extends from a lateral process of the notum (which I have designated the median notal process, fig. 2, D) to the spur of the posterior coxal fold.

Discs of the Pleural Wing Muscles.

In the Dytiscidae and Hydrophilidae I have examined, the most easily noticed difference in the structure of the thorax between the normal and the flightless form is to be found in the size of the discs of the pleural flight muscles. In all the species studied I have mounted the metatergum and pleura of a number of specimens (usually in polyvinyl lactophenol) inner side upwards to show the posterior or subalar disc, which from its position close to the edge of the notum is more convenient than the basalar for comparison with the size of the
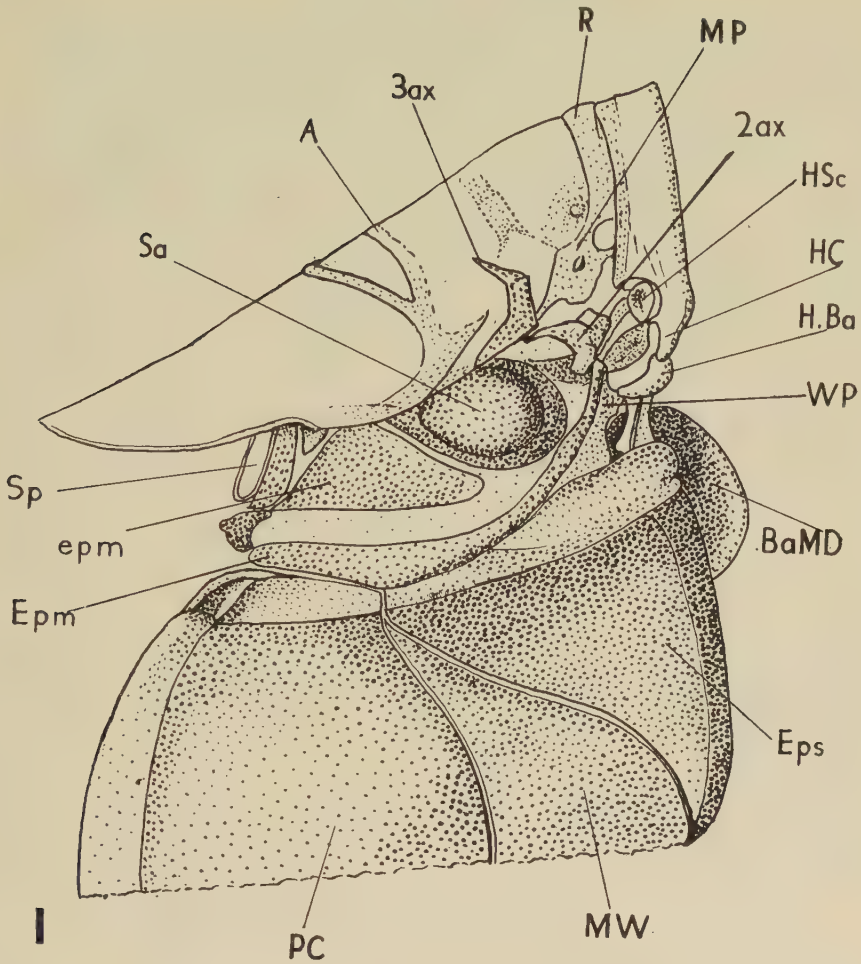
FIG. 1.—External view of right pleuron and wing base of *Agabus bipustulatus* Linn. The wing has been turned back over the metatergum and cut off.   × 30.

A, anal vein.
ANP, anterior notal wing process.
AP, apical plate of postnotum.
2ax, 3ax, second and third axillaries.
AxC, axillary cord.
Ba, basalare or parapterum.
BaMD, basalar muscle disc.
D, median notal process below lateral emargination.
Epm, epimeron.
epm, detached part of epimeron.
Eps, episternum.
H1ax, head of 1st axillary.
HBa, head of basalare.
HC, head of costa.
HSc, head of subcosta.

MDP, muscle disc on prescutum of musculus relaxator alae.
MP, median plate.
MW, metasternal " wing."
PC, post-coxa.
PN, postnotum.
PNP, posterior notal wing process.
PR, pleural ridge.
R, radius.
Sa, subalar disc.
Sc, subcosta.
Sp, spiracle of 1st abdominal segment.
WP, wing process.
X, small plate connecting epimeron with apical plate of postnotum.
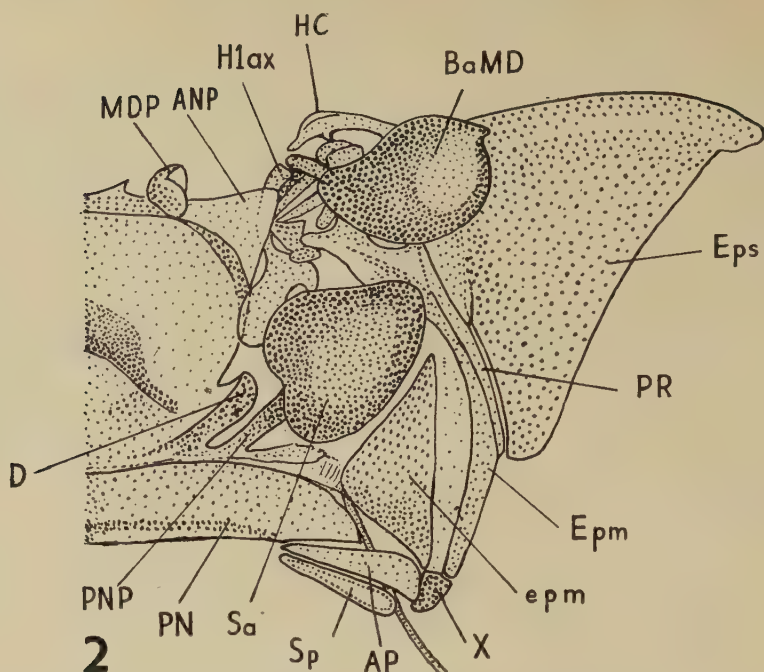
FIGS. 2–3.—(2) Internal view of lateral area of metatergum and left pleuron of *A. bipustulatus* Linn. × 30.   (3) Internal view of lateral area of metatergum and left pleuron of *Platambus maculatus* Linn.   × 45.
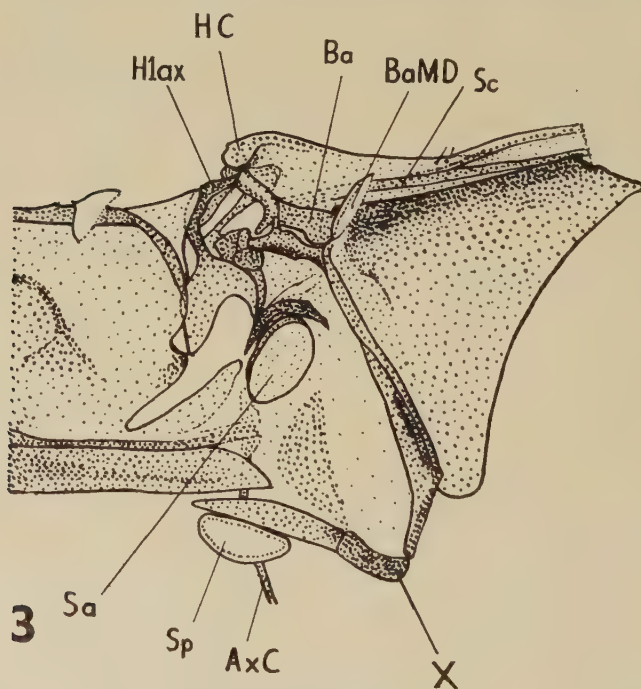
In Figs. 2 and 3 the basal part of the wing lies beneath the pleuron but is only shown in parts (costa and subcosta, axillary sclerites and axillary cord) to avoid complication.

For explanation of lettering see fig. 1.

metanotum. In all Dytiscidae studied this is the larger of the two discs, but in the Hydrophilidae examined the basalar disc is the larger. The position of these discs and their relation to the wing base, in an external view of the side of the metathorax, in a cleared specimen of *Agabus bipustulatus* is shown in fig. 1, and the difference in the relative size of the disc between this species and *Platambus maculatus* is shown in figs. 2 and 3. The relation of these discs to the wing base and the pleural wing muscles is clearly shown by Snodgrass (1935 : 232, fig. 129). I wish to express my thanks to Dr. Snodgrass for his kindness in examining a specimen of *Agabus bipustulatus* which I sent him, and for his help in naming the discs and adjacent parts of the thorax in this species, as shown in my figures. The basalar disc was formerly known as the parapteral or pronator muscle disc, and is so designated in his paper (1909), in which useful figures are given of the thorax of *Dytiscus*.

In the newly emerged beetles of the good-flying species the discs do not attain their full size until the beetle is hard, but in such soft specimens the flight muscles have been found to be fully developed, and if the young beetle is placed in dry conditions it usually flies away. If flightless beetles are exposed to dryness when soft they are unable to escape by flight, and the elytra may buckle and the wings become crumpled. It is interesting to find that in *Noterus clavicornis* with short wings and no flight muscles the subalar discs still persist but are very small.

The results of this study of the muscle discs and the flight muscles of Dytiscidae and Hydrophilidae show that when fully developed flight muscles are present these discs are large and strongly developed, and the prephragma and postphragma are well formed. The presence of small discs (in specimens no longer soft) is strong evidence that the flight muscles are imperfectly developed. In the Dytiscidae the subalar discs can usually be distinguished in freshly killed beetles (or in those preserved in alcohol) by removing the elytra and raising the wings, when, if darkly pigmented, they show quite clearly in the thin, transparent cuticle beneath the wing bases.

Capacity for Flight of Some Other Species.

In addition to the species already mentioned which fly readily, a few examples of the following species have been dissected which have also had perfect flight muscles and those which have been seen to fly are marked with an asterisk : *Hygrobia hermanni* Fab.* (from Yorks. and Norfolk), *Laccophilus minutus* L., *Hygrotus (Coelambus) confluens* Fab. (from Herts. and Yorks.), *Deronectes griseo-striatus* Deg. (from Morayshire), *Hydroporus angustatus* Sturm, *H. incognitus* Sharp,* *H. lepidus* Ol.,* *H. nigrita* Fab.,* *H. tessellatus* Drap.* (from Yorks. and Herts.), *Agabus chalconatus* Panz. type form (from Herts.) and var. *melanocornis* Zimm.* (a male of this variety was netted on the wing on a sunny day near Drumgask, Newtonmore, on 5th October, 1945, and another specimen from Fife flew when tested in July, 1951), *A. biguttatus* Ol.* (from Morayshire, seen to fly by Dr. Richter), *A. conspersus* Marsh. (from Prof. Balfour-Browne, locality not stated), *Ilybius ater* Deg., *Rantus bistriatus* Berg.,* *R. exsoletus* Forst.,* *Acilius sulcatus* L.,* *Octhebius marinus* Payk., *Limnebius truncatellus* Thunb.,* *Laccobius biguttatus* Gerh., *L. minutus* L.,* *Berosus signaticollis* Charp. (from W. Suffolk and Herts.) and *Hydrochus angustatus* Germ. (from Herts.).

Only a few Haliplidae have been dissected. In these quite well-formed discs are present, but the condition of the flight muscles is somewhat variable. A few have been seen to fly. These are *H. lineolatus* Mann., *H. lineatocollis* Marsh., *H. ruficollis* Deg., and *H. fulvus* Fab. Little investigation has yet been made of the Gyrinidae. The beetles of this family present many peculiarities of structure associated with their life on the surface film. The arrangement of the metathoracic muscles in the few species I have examined is very different from that occurring in the other families owing to the enormous development of the tergo-sternal muscles. The metathorax shows considerable modifications in structure, and, correlated with the small size of the pleuron, which is narrow in its dorso-ventral aspect, the pleural flight muscles are small and short and only one small disc has been distinguished with certainty. Both *Gyrinus natator* var. *substriatus* Steph. and *G. minutus* Fab. fly readily, and a few *G. marinus* Gyll. tested in October were seen to fly, and Dr. Richter informs me that he has seen *G. caspius* Men. fly. Of *Orectochilus villosus* Müll., a species of nocturnal habits, I have only obtained one specimen (from Loch Awe, Argyllshire), and its wings are fragile and much smaller in proportion to its size than are those of the other Gyrinids examined, and the metatergum is shorter, so I am doubtful if it could have flown.

Occurrence of Beetles in Localities indicating Recent Flight.

It would be of much interest to know more about the occurrence of species of water-beetles in tanks, troughs and other receptacles to which access by crawling from the ground is impossible. In such situations I have taken *A. bipustulatus*, *H. planus*, *H. pubescens* and *H. nigrita* and *Helophorous brevipalpis* —all good-flying species which are common in stagnant water. *H. brevipalpis* is one of the readiest beetles to fly, and will often fly off the net as soon as it is brought out of the water. Dr. Richter (1951) notes that *A. bipustulatus*, *H. pubescens* and *H. planus* are early colonists of newly formed waters. Prof. Grensted (1939) has made interesting observations on the arrival of water beetles in a canvas tank in his garden at Oxford. The vast majority were *H. brevipalpis*, and *Hydroporus planus* and *H. pubescens* came next in numbers. Dr. Macan (1939) records the beetles captured during six years in a fountain basin at Cambridge which was cleaned out several times a year. The majority taken were *Colymbetes fuscus* and *H. planus*, while next in number were *A. bipustulatus*, *A. nebulosus* and *H. pubescens*, all species which I have included in my list of the most ready fliers. In a cement pool in a park at York which had been cleaned out in the " back-end " I took in April this year, with the help of Mr. Smith, the following beetles : *H. planus* 13, *H. pubescens* 6, *H. nigrita* 1, *H. tessellatus* 2, *A. nebulosus* 4, *A. bipustulatus* 1, *C. fuscus* 1, *I. fuliginosus* 1, *Gyrinus natator* 5, all good fliers. A single specimen of *Oreodytes halensis* Fab. was also taken (a species noted by Dr. Macan from the Cambridge fountain basin), so it must also be capable of flight.

Observations on the colonisation of newly flooded areas would be helpful, especially if the ground flooded had been free of springs and marshes. The investigations made by Mr. E. S. Brown on the colonisation by animal life of a freshly filled pond in Hertfordshire which had been empty for a few years are of great interest (1951). His results bear out my observations on *Noterus*. He states that neither species of *Noterus* had appeared in the pond, although both

occurred in the area within two or three miles, one of them, *N. capricornis*, being quite common.

Some species of water beetles are known to fly at night, e.g., Haliplidae (Hickman, 1931) and various Dytiscidae (Sherman, 1913). The latter author states that many Hydrophilidae are collected at light even in the desert region great distances away from any known water supply. Dr. C. B. Williams has sent me a male *Dytiscus marginalis* taken in a light-trap at Rothamsted Experimental Station, Harpenden, on 12.vii.49. Wesenberg-Lund (1912) states that he has only rarely seen the large Dytiscidae flying over seas and lakes, but on fine autumn days he has seen *Acilius* flying in the sunshine and plunging into the water of small moorland ponds. He also refers to the capture of a *Dytiscus* in the middle of the North Sea. Bertrand (1943) states that *Cybister lateri-marginalis* Deg. and *Colymbetes fuscus* have been collected in the sea, and he concludes they have flown there, attracted by the shining surface of the sea at night.

DISCUSSION.

I consider that beetles with abnormal flight muscles are individuals in which the normal development of the flight muscles and their supports has been arrested at an early stage, as was suggested in my studies of flight muscles of *Sitona* weevils (1933). Whether the failure of the flight muscles and their supports to develop fully is an hereditary character or whether it is influenced by environmental conditions during ontogenetic development is unknown. In the weevil *Sitona hispidulus* Fab. a similar variation was found to occur in regard to the development of the muscles of flight as is here recorded for a number of water beetles, some weevils being able to fly, while others were flightless, and the chitinous supports of the flight muscles showed similar modifications in the flightless weevils. In the course of breeding experiments with *Sitona hispidulus* it was found that there was a marked increase in the proportion of flightless forms amongst those reared in captivity, and that the individuals emerging late in the season were all flightless. Moreover, from a study of weevils collected in different localities, it was found that a higher proportion of flightless forms occurred in the north of Scotland than in England and Wales. It was thought that unfavourable environmental conditions were responsible for the flightless beetles. Much more investigation is required in regard to the distribution of the normal and the flightless form in those water beetles in which the flight muscles show variation in development. Are these beetles for instance more often flightless in Scotland than in the south of England? My dissections of *Hydroporus palustris* showed that out of 15 specimens from Hertfordshire only one had abnormal flight muscles, but out of 87 collected in Fife, 57 had the flight muscles imperfectly developed. However, nine of the Hertfordshire specimens were young beetles (with immature reproductive organs and often with soft cuticle), while of the Fife beetles only 23 were young, and the flight muscles in variable species have been found to be more frequently well developed in young specimens, as has been already mentioned. But even allowing for this the numbers are significant, and it is hoped to obtain more *H. palustris* from the south to continue this investigation. It would be interesting also to know if beetles emerging late in the season are liable to be flightless in variable species,

and if there is any increase of flightless forms in a late season. It is clear that only certain species of water beetle are subject to this marked variability in regard to the development of the flight muscles, others being capable of flight at all times, while others appear to be permanently flightless and a few may even be brachypterous. It is surely in these variable species that the first stage in the process of flight reduction is exhibited ; whether or not flightlessness is successful will be determined by natural selection.

More investigations are required into the habits of water beetles. It is probably only amongst those species which have already adopted habits rendering them independent of flight that a reduction of the organs of flight will have survival value. Then, loss of flight muscles would be an advantage to the species by affording more space for fat body and for the development of the reproductive organs. Once the flight muscles have become ineffective, wings will have become redundant, and any mutation resulting in their reduction will be an advantage to the species. Darlington (1943), who has studied flight reduction in Carabidae, concludes that if flight becomes useless to a species it will be an advantage to the species to have reduced wings, as such insects will have simpler structure, simpler metamorphosis, and lower energy requirements than fully winged forms. Professor C. H. Waddington states (1950 : 297) : " Probably the main connection in which mutation pressure has any influence on the course of evolution is in causing the reduction of organs which are no longer of any adaptive significance ; in total absence of selection, random mutations can accumulate."

How far is the loss of flight a factor of importance in regard to the distribution of species ? Until much more is known regarding the frequency of flightlessness amongst water beetles it would be premature to discuss its possible effect on the distribution of any particular species. It is clear, however, that the distribution of a flightless species will be largely dependent on how well distributed the species has been before the onset of flightlessness. Before the time of drainage and cultivation water beetles must have had optimum conditions for dispersal, and where the habitats have remained unaltered, as in lakes, rivers and swamps, flightless species may be expected to persist. It seems unlikely, however, that they would be able to colonize new areas unless accidentally transported (and here flooding may be a factor of importance), but in damp surroundings they may be able to spread to a limited extent by walking. Flightlessness, once established, would be a check to the further distribution of a species, but if rare flying forms persist a slow spread would be possible. My investigations show that some of the most widely distributed species are those in which the flight muscles are very well developed. A few species which are local have also been found to have perfect flight muscles, and it is certain that many factors besides capacity or incapacity for flight are concerned in the distribution of species ; in fact it is probable, as already suggested, that flightlessness has arisen amongst species which have already become fixed in habit and habitats which render flight unnecessary. It is hoped that more light will be brought to bear on some of these problems by the observations of other workers, who may already have helpful data to contribute regarding the flight of water beetles.

I would be very glad to receive living beetles or those preserved in alcohol of any of the species recorded above as without normal flight muscles, and specimens from abroad would be especially welcome.

Summary.

Investigations have been made into the condition of the flight muscles in a number of species of water beetles, principally the Dytiscidae and some Hydrophilidae.

Many species examined have been found to have well-developed flight muscles at all times of the year, and a number have been seen to fly in tests carried out.

In other species, mostly of the Dytiscidae, the development of the flight muscles has been found to be abnormal, the fibrous muscles of flight being absent, or represented by greatly reduced fibres of abnormal histology. In such species modifications occur in the structure of the metathorax, and the discs of the pleural flight muscles are small and weakly developed.

In a number of species the condition of the flight muscles has been found to be variable in different individuals, some being capable of flight and others flightless. The flightless individuals may show similar modifications of the metathorax and muscle discs to those which occur in the flightless species, but in some individuals the muscles alone show reduction. It is possible that in such individuals the flight muscles were at first fully developed and later underwent degeneration, as it has been noticed that a higher proportion of forms capable of flight occur amongst the newly emerged beetles.

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Appendix.

Since the completion of this paper Dr. Richter has very kindly sent me some water beetles, preserved in alcohol, which he has collected at Salem, Baden, in southwest Germany.   The species include several which I have reason to think are flightless, or usually flightless, in this country, and it is most interesting to find that the German specimens show just the same modifications.   Thus with *Laccophilus hyalinus*, those I have dissected have abnormal flight muscles and the same reduction of parts of the metathorax as I observed in the English specimens.   The same is true of *Platambus maculatus*, *Hyphydrus ovatus* and *Noterus capricornis*, while thirteen German examples of *N. clavicornis* have diminutive wings of varying size and shape, but all within the size range I have recorded (1950) in the British specimens.   Twenty-five *Orectochilus villosus* have been received, in all of which the wings are frail and of the same small size relative to the long body as already noted from the one Scottish specimen.   I scarcely think that they would support the body in flight.   Dr. Richter writes that he " could not make *Orectochilus* fly by confining them in a box for some hours and then opening them, which usually works with *Gyrinus*," but he has observed that they can jump like *Laccophilus ;* he has seen *L. hyalinus* jump more than a foot.   Species he has seen to fly, not recorded in my paper, are *Rantus pulverosus* Steph., *R. frontalis* Marsh. (*notatus* Fab.), *Hydrochara caraboides* (L.) and *Hydrophilus piceus* L.

Book Notice.

The Observer's book of the larger British moths. By R. L. E. Ford.   12mo. London (Warne), 1952.   Pp. 224, text illust. (some col.).   Price 5s. 0d.

This pocket guide covers the Super-families Sphinges and Bombyces, comprising 104 species, to which have been added nine of the largest representatives of other families, all illustrated in colour, together with 86 half-tones of eggs, larvae and pupae.

The descriptions are short, but brief field notes have been added in all cases. An index of English and Latin names completes the book.

THE PLECOPTERA OF THE ISLE OF MAN.

By H. B. N. Hynes, Ph.D., F.R.E.S.

(Department of Zoology, University of Liverpool.)

During the course of other work on the freshwater fauna of the Isle of Man records have been kept of the occurrence of stoneflies, and these insects have been searched for whenever possible. Now that a considerable number of collections has been made several points of interest have emerged.

My visits to the island have all been made in January, April and July, and most of the specimens are nymphs, but I have been fortunate in obtaining several collections of adults made in May and early June, 1951. My samples contain adults of eight of the ten species collected, and there is little doubt that all the nymphs have been correctly identified.

I am very much indebted to Dr. N. S. Jones of the Marine Biological Station, Port Erin, who has not only made, at my request, the collections of adults mentioned above, but has assisted me on many occasions with transport and has helped me in many other ways. I am also most grateful to Dr. W. E. Frost of the Freshwater Biological Association, who has put at my disposal collections of stoneflies made in Ireland by herself and the late Mr. R. Southern. These collections, although extensive, contain no species not already listed by King and Halbert (1910), and so confirm the fact that the plecopteran fauna of Ireland is somewhat limited.

Stations Collected.

The island, which lies in the Irish Sea about 16 miles from Ireland, 18 from Scotland and 30 from England, is fairly mountainous, except in the north, where the country is flat and swampy. There are abundant small permanent stony streams, flowing through wooded valleys, or across agricultural land, in their lower courses. Four of these streams, the Sulby River, the Douglas River, with its two tributaries the Dhoo and the Glass, the Silver Burn and the River Neb, attain the proportions of small rivers, but all have rocky or stony beds and a fairly rapid flow. These waters are therefore apparently ideal habitats for stoneflies, and correspond closely to the types of stream investigated in the English Lake District (Hynes, 1941). There are no natural lakes on the island, and the only large bodies of still water are several reservoirs made by the damming of streams ; these have not been investigated.

British species of stoneflies emerge in the spring and early summer or in the latter part of the summer (Hynes, 1940). It is therefore possible to collect fairly well-grown nymphs of all species by making collections in the winter or early spring and in the summer. The present investigations were made in January, 1951, April, 1949, 1950 and 1951 and July, 1949. It is therefore to be expected that, as the collections were extensive and for most localities thorough, nymphs of all species, or at any rate of all common species, present in the island will have been obtained.

The table shows the localities where stoneflies were found ; some localities were very thoroughly searched for these insects without result. The stream names in italics do not appear on the one-inch Ordnance Survey map of the island, and are either in current use by the islanders or have been given

to the localities by the author.   When this has been done the name of the nearest house or natural feature has been given to the stream.   It has not unfortunately been possible to give the National Grid References to the localities, but they are all shown by numbers on the map.   In the last column of the table the letter W

Map No.	Name of locality.	D. bicaudata.	C. tripunctata.	C. torrentium.	L. hippopus.	L. inermis.	L. fusca.	P. meyeri.	A. sulcicollis.	N. cinerea.	N. inconspicua.	
1	Sound stream						+					WS
64	Port Erin stream			+								WS
65	Port Erin tributary			+	+					+		WS
63	Spaldrick stream											WS
62	Fleshwick stream			+	+	+			+			WS
66	Harbour Master's stream											WS
3	Gansey stream				+				+			WS
5	Colby river			+			+	+				WS
8	Strandhall stream											WS
9	Arbory stream			+	+	+		+	+			WS
10	Ballabeg stream			+	+							WS
11	Poyllvaaish stream											WS
18	Silver burn	+	+	+	+	+	+	+	+			WS
12	Grenaby stream		+	+		+	+	+				WS
16	St. Mark's stream			+			+	+	+			WS
21	Ballalona stream					+						WS
20	Santon burn							+				WS
23	Glen Grenaugh				+	+		+	+			WS
24	Crogga river			+	+	+		+	+	+		WS
25	Richmondhill stream			+		+	+					WS
27	River Dhoo					+	+				·	WS
52	River Neb	+	+	+	+	+	+	+	+			WS
2	Glenchass									+		W
7	Ballagarmin stream				+				+			W
19	Ronaldsway stream									+		W
17	Ballasalla stream			+								W
46	Bishops Glen	+		+	+	+			+			W
44	The Lhen											W
61	Croggenmooar stream			+	+			+	+			W
60	Balladha stream				+				+			W
45	Killane river									+		W
58	Headwater of Glen Rushen							+				W
29	River Glass						+					S
30	Sulby river Abbeylands	+					+					S
26	Douglas river						+					S
55	Foxdale river						+					S
57	Glen Maye						+					S
53	Shenvalla stream						+					S
54	Ballamoore stream						+					S
50	Ballabooye stream						+					S
49	Ballaguine stream		+				+					S
48	Cammall stream						+	+				S
47	Glen Wyllin						+					S
51	Ballagyr stream						+					S
33	Glen Groundle						+					S
38	Ballure stream						+					S
40	Sulby river						+					S
43	Headwater of Sulby river	+	+	+				+		+	+	S

indicates that collections were made either in January or April or in both, and the letter S indicates that collections were made in July. *Leuctra fusca* would not normally be found in the winter and spring collections, and most other species would not usually be found in July.
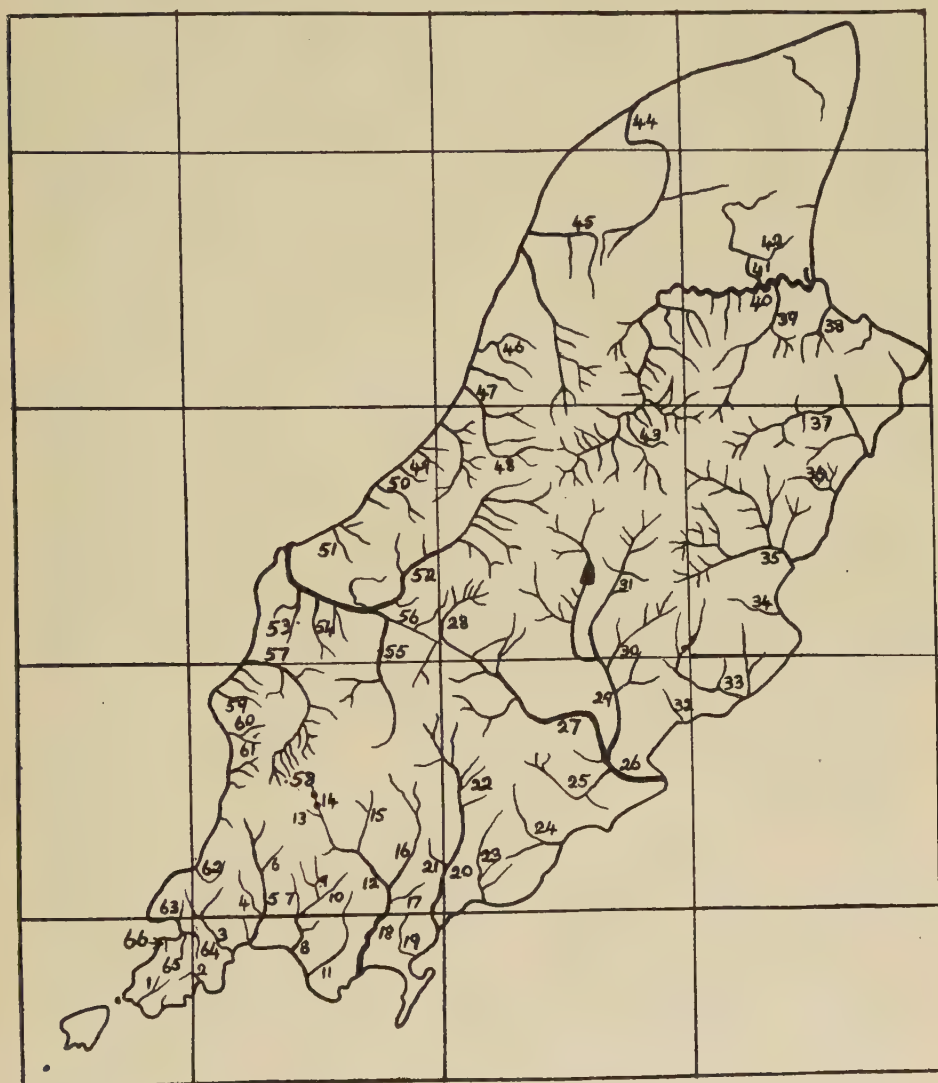
Plecoptera of the Isle of Man. The table on p. 72 gives a key to the locality numbers and distribution of species.

In addition to the 48 localities shown in the table the following 18 localities were sampled in July without result : two tributaries of Colby river (4 and 6) *Garey Mooar stream* (13), *Cringle stream* (14), *Clougher stream* (15), *Ballahowin stream* (22), Greeba River (28), Baldwin River (31), *Governor's Bridge stream*

(32), Garwick Glen (34), Laxey River (35), Dhoon Glen (36), Glen Corna (37), Glen Aldwyn (39), *Garey stream* (41), *Boliviamount stream* (42), *Scravorly stream* (56), and *Ballelby stream* (59).

It will be seen that the 66 localities are widely scattered over the island, but that most of those investigated in January or April lie in the southern half of the island.

Species Collected.

Diura bicaudata (L.) was found in only six streams, including four at little above sea level and one high stream (*circa* 1000 ft.). It was not common in any of the places where it was found, and it probably was present but not found in other streams also. The lowland localities were fast-flowing rivers or medium-sized streams.

Chloroperla tripunctata (Scopoli) was found only in three swift rivers and in the high stream with *D. bicaudata*. It was abundant where found, and it probably occurs also in the River Glass and the Sulby River, which appear to offer suitable habitats, but which were only investigated in the summer, after the emergence of the adults. It was not found in any small lowland streams, although it has been recorded from such streams in England (Hynes, 1941). The nymphs seemed to be associated with clean gravel where the current was swift.

Chloroperla torrentium (Pictet), in contrast to the last species, was found in sixteen localities of very varied types, on clean, silty and mossy substrata, in swift and relatively sluggish water, and at high and low altitudes.

Leuctra hippopus Kempny was found in thirteen localities of various types, but appeared to be associated with silt, vegetable debris or moss. Unlike *L. inermis* the nymphs were not often found in clean gravel. Jensen (1951) suggests that this species is stenothermic in Denmark, but this does not seem to be so in the Isle of Man, nor in England (Hynes, 1941).

Leuctra inermis Kempny was found in eleven localities of varying types, but the numphs were found chiefly in clean areas of gravel away from silt and vegetable matter.

Leuctra fusca (L.) was found in twenty-three localities of very varying types. It appeared to be absent from several streams in the south of the island which were very thoroughly searched.

Protonemura meyeri (Pictet) was found in thirteen localities, most of which were medium-sized or large streams, and the nymphs were definitely associated with mossy patches of substratum.

Amphinemura sulcicollis Stephens was found in thirteen localities, in all of which there was moss or overhanging grass. The streams in which it occurred were of all sizes.

Nemoura cinerea Retzius was found in six streams, five of which were noticeably silty and rather sluggish. The sixth was a high stream with boggy banks. The nymphs were found under stones and amongst vegetable debris. No adults of this species were obtained.

Nemurella picteti (Klapálek) was taken only on one occasion, in a small high stream, and only a single nymph was obtained. The nymph was collected in July, but none was found in five similar streams investigated in the same month. Jensen (1951) suggests that in Denmark this species occurs only in

cold water, which may account for its absence at lower altitudes on the island, although it has been found at low altitudes in the Lake District.

DISCUSSION.

It will be seen from the above data that the species found on the island occupy more or less the same types of habitat as have been found previously (Hynes, 1941), but several points of interest emerge from this study.

Firstly there appear to be only ten species present, despite the apparent suitability of the available rivers and streams for other British species. Apart from *D. bicaudata* no short-winged species occur. The absence of *Perla carlukiana* Klapálek, *P. cephalotes* Curtis and *Perlodes mortoni* Klapálek is particularly striking, as localities which appear very suitable for these species occur in the four rivers. Similarly there appear to be no species of *Capnia*. Both species of *Perla*, *P. mortoni* and two species of *Capnia* occur in Ireland (King and Halbert, 1910), and *Perla* spp., *P. mortoni* and *Capnia bifrons* Newman occur commonly in Scotland, England and Wales.

According to Lamplugh (1903) the Isle of Man was completely glaciated during the ice-age and has not since had any land connection with other parts of the British Isles. Presumably, therefore, the present fauna has reached the island across the sea. This suggestion is supported by the absence of any exclusively freshwater fish (Crellin, 1879). This would, therefore, account for the absence of short-winged species of stonefly. *D. bicaudata* is, however, an exception, and is perhaps also a special case. This species is northern in distribution, occurring in both Eurasia and North America (Brinck, 1949). It also seems to be able to withstand extreme cold, as it occurs in lakes in Swedish Lapland (Brinck and Wingstrand, 1949), and in the far north of Canada, where it is known as *D. postica* (Walker) (Ricker, 1944). It is possible that this species may have crossed the ice to the island during the glacial period as, it is surmised, did the Irish Elk (Lamplugh, 1903). There is another species which might have come in the same way, *Capnia atra* Morton. This also occurs in cold lakes (Brinck and Wingstrand, 1949), and is present in Ireland (King and Halbert, 1910) and Scotland (Brown, 1945), but as this species appears to be almost confined to lakes (Brinck, 1949, and Kimmins, 1950) there is at present no suitable habitat for it on the island.

More inexplicable is the absence of several winged species, in particular *Isoperla grammatica* (Poda), *Leuctra nigra* (Olivier), *L. geniculata* (Stephens), *Nemoura cambrica* Stephens, *Protonemura praecox* (Morton) and *Brachyptera risi* (Morton), all of which are able to fly and are common on the British mainland in habitats which appear to be similar to those available on the island. Of these species *I. grammatica*, *B. risi* and *P. praecox* occur also in Ireland (King and Halbert, 1910). It would appear therefore that the present stonefly fauna is a chance assemblage of species which have somehow managed to cross the sea. Balfour-Browne (1911) states that the list of Manx water-beetles suggests a closer affinity with the fauna of North-West England than that of other neighbouring countries, but this cannot be stated for the stoneflies, as all the Manx species occur in England, Scotland, Wales and Ireland.

A second feature of interest is the presence in lowland streams of *D. bicaudata*. On the British mainland, and apparently also in Ireland, this species is confined to lakes and high streams, the lower parts of streams being occupied by *P.*

mortoni (Hynes, 1941).   *P. mortoni* being absent from the Isle of Man, it may well be that the peculiar distribution of *D. bicaudata* elsewhere is due, not to its being stenothermic, as was suggested previously (Hynes, 1941), but to its being unable to compete with *P. mortoni* in running water at low altitudes. That both species can occur together has, however, been shown by Jones (1949), who found them at three stations between 200 ft. and 800 ft. in the River Rheidol in Wales.   Dr. Jones lists *D. bicaudata* as *Isogenus nubecula* Newm.?, but he has kindly allowed me to examine some of his specimens, and they are definitely *D. bicaudata*.   It is noticeable that he found very few specimens of *D. bicaudata* at these stations, whereas *P. mortoni* was much more common. Perhaps these specimens had been washed down from higher altitudes and were able to survive, despite the presence of *P. mortoni*, because of the large size of the river.   It is, however, difficult to speculate in the absence of any knowledge of the nature of any possible inter-specific competition.

Finally it is interesting to note that five of the streams which were thoroughly investigated were found to contain no stonefly species.   These streams had no obvious common features, and would appear to be suitable for some species. This and the apparent absence of some other species from some of the other streams remain unexplained.

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A STUDY OF THE LIFE CYCLES AND GROWTH-RATES OF FOUR SPECIES OF MAYFLIES.

By Janet E. Harker, M.Sc., Ph.D., F.R.E.S.

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The life history of few mayflies is completely known, although numerous records have appeared, mainly from anglers, of the emergence dates of the imagines.

Rawlinson (1939) found that there were two broods of *Ecdyonurus venosus* (Fab.) a year, and also found a marked seasonal difference in the growth-rate. Moon (1938) estimated the growth-rate of two species of *Leptophlebia* and of *Caenis horaria* (L.), and showed that there is a single brood each year of all three species.

METHOD.

This investigation was carried out on *Ecdyonurus torrentis* Kimmins, *Heptagenia lateralis* (Curtis), *Rithrogena semicolorata* (Curtis), and *Baetis rhodani* (Pictet) from Wayoh Stream near Bolton, Lancashire. The life cycles were determined by measuring a series of nymphs each month, and also by collecting imagines as they emerged.

Collections were made by holding a net in the stream, upturning stones or otherwise disturbing the bottom on the upstream side, and allowing any animals present to be washed into the net. Collecting was carried on for a period of ten minutes in each of the various types of habitat present. No constant number of nymphs was collected using this method, but it was thought to be the best means of obtaining random collections.

The nymphs were measured on microscope slides, care being taken to prevent their drying as this caused contraction. Measurements were taken from the anterior edge of the clypeus to the base of the caudal cerci and were made to the nearest millimetre. All nymphs above two millimetres in length were measured : nymphs below two millimetres could not be identified with any certainty and they were difficult to separate from the rubble collected in the net.

Ecdyonurus torrentis Kimmins.

The percentage of nymphs of *Ecdyonurus torrentis* in each length class, measured from September, 1949, to June, 1951, is shown in fig. 1.

In September, 1949, the highest percentage of nymphs occurred in the 7 mm. class, 40 per cent. of the nymphs being in that class. Only 25 per cent. were in the 6 mm. class and nymphs in the 4 and 5 mm. classes were comparatively rare ; 24 per cent. and 28 per cent. were present in the 3 and 2 mm. classes respectively. This indicates that two main groups were present, and it is possible to trace these through the subsequent records, month by month, until March, 1950. The group of larger nymphs then disappeared ; it seemed likely that this was due to emergence, an interpretation which was confirmed by the presence of adults. At the same time a high percentage of nymphs less than

5 mm. in length made their appearance. Since nymphs of this size had been absent since January, 1950, it would appear that they had been produced from newly laid eggs, and this is confirmed by the fact that adults are present at this time.

In April, 1950, there were still two size groups of nymphs present; 14, 9 and 7 per cent. were present in the 2, 3 and 4 mm. classes respectively; no nymphs were obtained in the 5, 6 and 7 mm. classes; the rest measured between 8 and 15 mm., with the greatest numbers in the 8, 9, and 10 mm. classes. The group of larger nymphs can be traced as those nymphs which formed the smaller
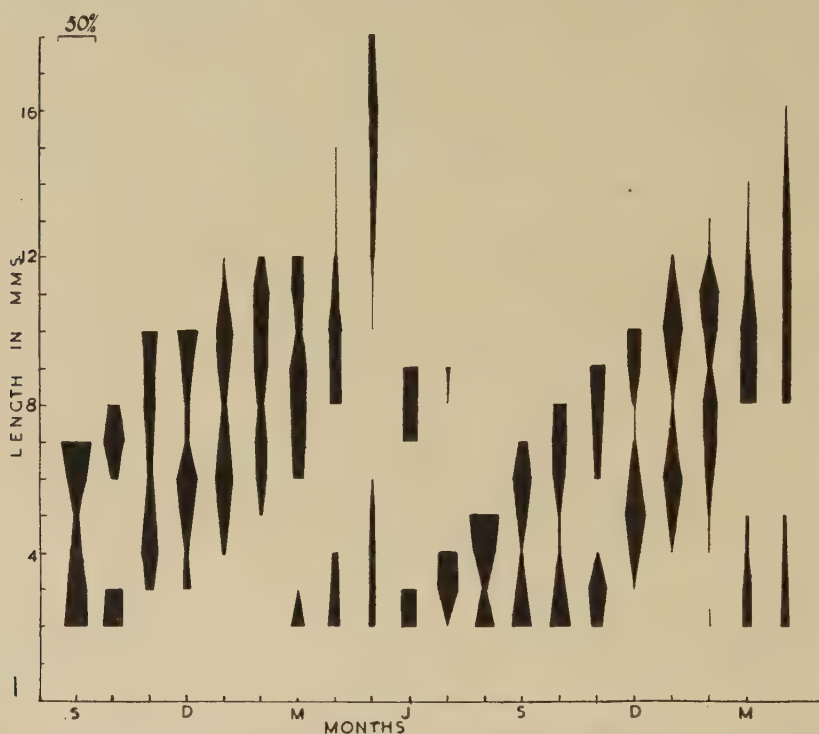
Fig. 1.—The monthly percentage of nymphs of *Ecdyonurus torrentis* Kimmins contained in each millimetre length class.

size group from September to March. In May these larger nymphs disappeared, and again it seems probable that this was due to emergence. Imagines were collected and an increase to 22 per cent. in the 2 and 3 mm. classes in June, as compared with 8 per cent. and 7 per cent. in the previous month, implies a new batch of nymphs.

In June 19 per cent. and 22 per cent. of the nymphs were in the 2 and 3 mm. classes, and 18, 19, and 19 per cent. in the 7, 8, and 9 mm. classes respectively. The 7, 8, and 9 mm. nymphs can be traced back to the small April nymphs. In July the group of larger nymphs disappeared and adults were collected; in August the percentage of 2 mm. nymphs rose to 26 per cent. as compared with 1 per cent. in July. Again it is probable that the larger

nymphs had emerged in July, and newly laid eggs had produced the increased number of small nymphs present in August.

In August, 1950, two sizes of nymphs, similar to the two size groups which were first observed in September, 1949, were collected ; 26 per cent. of the nymphs were in the 2 mm. class and 4 per cent. in the 3 mm., 30 per cent. and 40 per cent. being in the 4 and 5 mm. classes. These two groups can be traced through the months until March, 1951, when again the group of larger nymphs disappeared, and a group of nymphs less that 5 mm. in length reappeared.

FIG. 2.—A diagram of the seasonal life cycle of *Ecdyonurus torrentis* Kimmins. The arrows indicate the hatching of successive broods.

The length classes showed the same two groupings in April, 1951, as had appeared in April, 1950. Again in May the group of larger nymphs disappeared and an increased percentage of small nymphs occurred in June, implying a new hatch of nymphs following an emergence of the imagines.

Measurements were discontinued in June, 1951, after having been obtained over a period of twenty-one months. From the results it appears that three broods of *E. torrentis* occurred in Wayoh stream throughout the course of the year, the nymphs of two different broods being present at any one time. The three broods fall approximately into the periods March–July, July–May, and May–March (fig. 2). How far overlapping between the broods occurs, due to individual differences in growth rate, cannot be estimated. It appears likely that this may occur to some extent.

The average growth per month within each size group can be calculated from the measurements of the lengths of the nymphs. A graph of the calcu-

lated average growth-rate is given in fig. 3. The growth-rate of the summer or March–July brood was greatest in June when the average growth was 3·3 mm. The rate dropped in the second month, May, from 2·7 to 2·0 mm., and again in July to 0·7 mm. The July–May brood showed a slower rate than the March–July brood. From August, 1949, to April, 1950, the rate varied between 0·1 and 1·2 mm. per month, and then prior to emergence
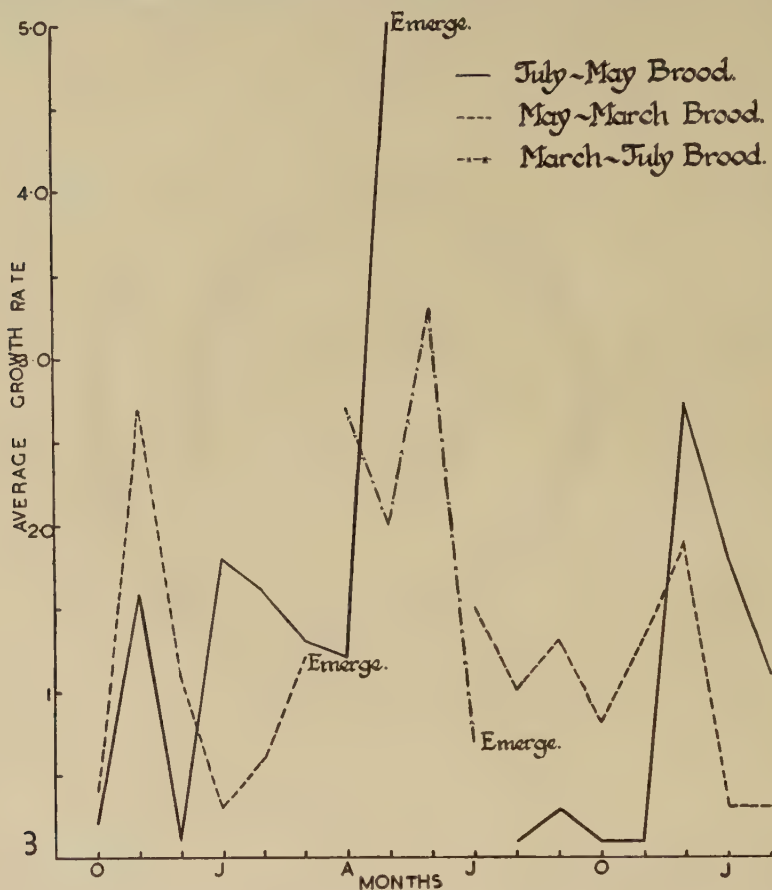
FIG. 3.—The average monthly growth-rate of the nymphs of *Ecdyonurus torrentis* Kimmins.

in May the rate rose suddenly to 5·0 mm. per month. The May–March brood had a rate intermediate between 0·3 and 1·2 mm. per month, except in November, 1949, when it increased to 2·7 mm. per month. From July, 1950, to February, 1951, the rate was fairly uniform, varying from 1·0 to 1·5 except in December, 1950, when the rate increased to 1·9 mm. per month.

Comparison of the growth-rate with the temperature of the stream shows an increase in growth in November in the July–May and May–March broods, when the temperature dropped from 10° C. to 5° C. The growth of the March–July brood increased from 2·0 to 3·3 mm. per month when the temperature rose above 10° C. Growth-rate of the July–May brood increased from an

average of 0·8 to 4·3 mm. per month from March to May when the temperature rose above 6° C. ; that of the May–March brood dropped from November to February, when the temperature was below 6° C., and rose to an average of 1·1 mm. per month when it was above 6° C.

These changes in growth-rate suggest a correlation between growth and temperature in the spring, but there appear to be other factors controlling growth in the autumn.

Nymphs of the July–May brood kept in the laboratory at room temperatures which were higher than those of the stream, emerged at the same time as the
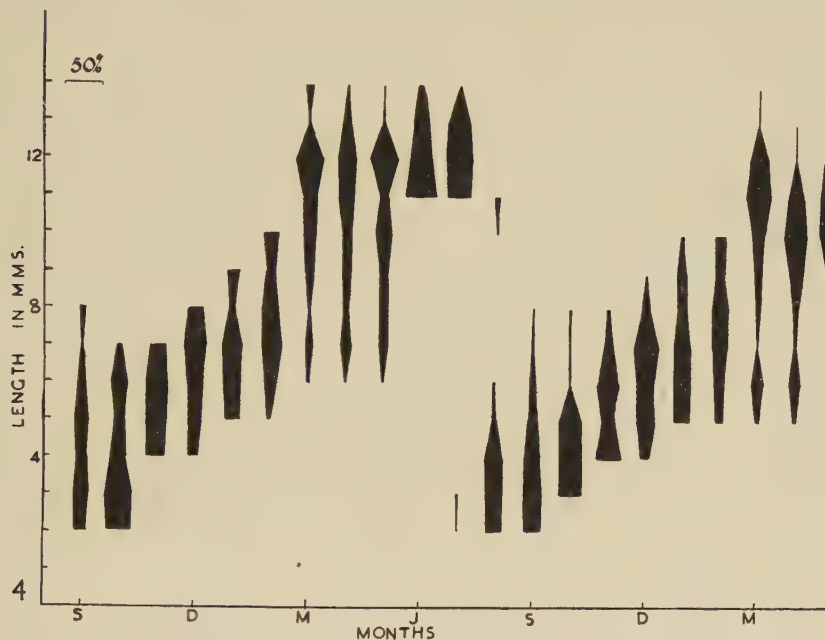
Fig. 4.—The monthly percentage of nymphs of *Rithrogena semicolorata* (Curtis) contained in each millimetre length class.

May–March brood nymphs kept under the same conditions. It is possible that, if the temperature rose early in the year, the July–May brood might emerge with the May–March brood, or conversely if it rose late in the year, the May–March brood might emerge with the July–May brood. It therefore seems likely that the number of broods per year is in part dependant on seasonal factors, and interbreeding between the three broods is probably not prevented by a well-marked time barrier.

Rithrogena semicolorata (Curtis).

The percentage of nymphs of *Rithrogena semicolorata* in each length class, measured from September, 1949, to June, 1951, is shown in fig. 4.

In September, 1949, the highest percentage of nymphs was in the 3 mm. class, 21 per cent. being present. Between 13 per cent. and 18 per cent. were in each of the 2, 4, 5 and 6 mm. classes. In October, 1949, 36 per cent. were

still in the 2 mm. class, but the percentage in both the 4 and 6 mm. classes had increased to 21 per cent. This gradual increase in size with a range over five or six millimetre classes can be followed month by month till March, when the variation in size increased to cover nine classes, the greatest percentage being in the 12 mm. class. This wide variation is apparent till May, but gradually the numbers become more concentrated, 70 per cent. being in the 10, 11 and 12 mm. classes. In June the variation only covered four classes, and of these only 6 per cent. were in the largest 14 mm. class. In July, 1950, 5 per cent. of the nymphs appear in the 2 and 3 mm. classes, and since no nymphs of this size have been present since October, 1949, it is probable that these small
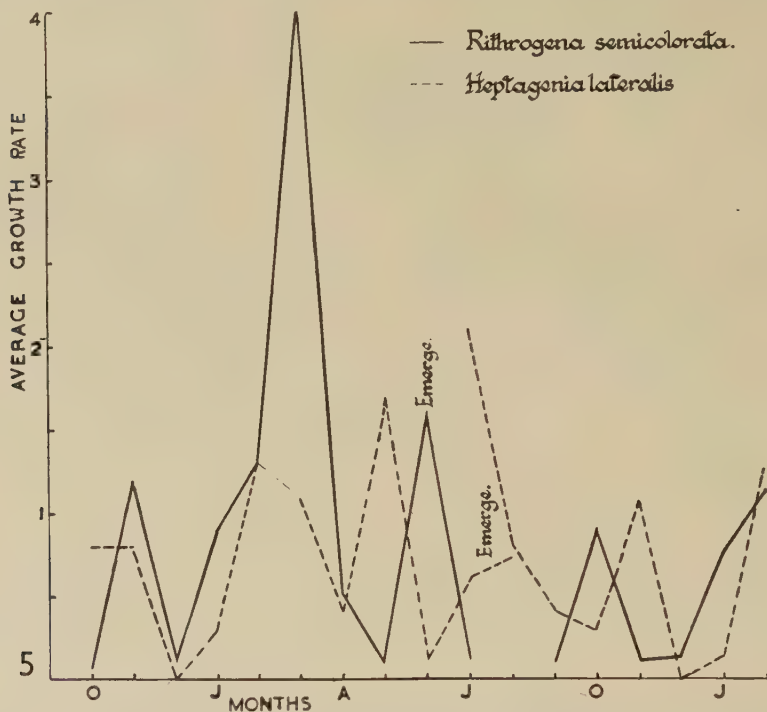
Fig. 5.—The average monthly growth-rate of the nymphs of *Rithrogena semicolorata* (Curtis) and *Heptagenia lateralis* (Curtis).

nymphs came from newly hatched eggs. In August all the nymphs above 11 mm. disappeared and the greatest numbers were in the 2, 3 and 4 mm. classes. These two facts together point to emergence having taken place in June and July. Adults were also collected at this time. By September, 1950, all the nymphs above 8 mm. had disappeared, so that it may be supposed no more adults emerged after that time.

The average growth per month has been calculated from the length measurements, and a graph of the calculated average rate is given in fig. 5.

The growth-rate is fairly uniform throughout the year, varying between 0·1 and 1·2 mm. per month, except in March, when it increased to 4·0 mm. per month as the temperature increased from 4° to 7° C., and in June when it

increased to 1·6 mm. per month as the temperature rose from 10° to 16° C. There are similar rises in temperature at other times of the year, but these do not appear to have the same effect as the increases in March. This suggests that a temperature level of about 6° C. is required for active growth. A similar condition appeared to exist for *E. torrentis.*

From these results it is concluded that *R. semicolorata* has a univoltine life cycle, but that emergence may be spread over some months and the time of emergence depends, at least in part, on seasonal factors.
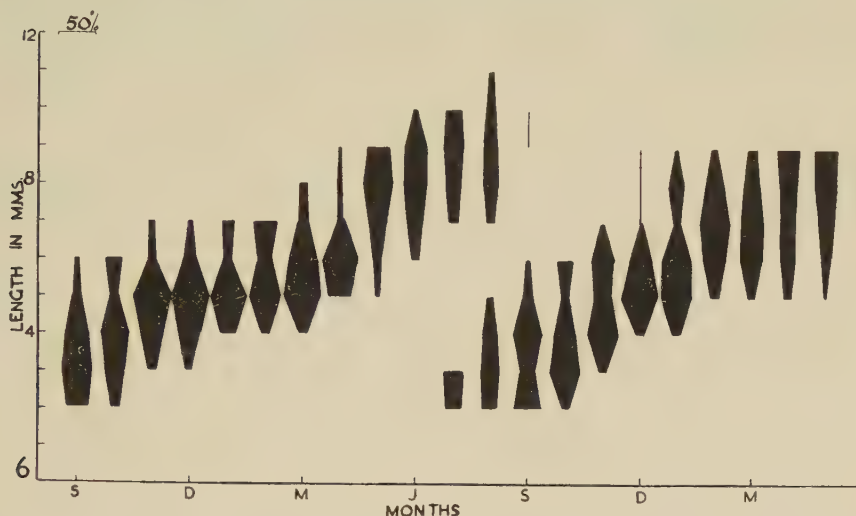
Fɪɢ. 6.—The monthly percentage of nymphs of *Heptagenia lateralis* (Curtis) contained in each millimetre length class.

Heptagenia lateralis (Curtis).

Measurements of the nymphal lengths between September, 1949, and June, 1951, appear in fig. 6.

In September, 1949, nearly all the nymphs were in the 2, 3 and 4 mm. classes, with 3 per cent. and 4 per cent. in the 5 and 6 mm. classes. In October, 1949, 30 per cent. and 38 per cent. were in the 3 and 4 mm. classes and 5 per cent. were in the 7 mm. class. This gradual movement into the larger classes is followed each month to June, 1950, with a variation within each month of four or five millimetres. In July 34 per cent. of the nymphs were in the 2 and 3 mm. classes, and, as no nymphs of this size had been present since October, 1949, it is probable that these were newly hatched. At the same time the percentage of nymphs in the larger classes fell, and this, together with the fact that adults were collected, suggests that emergence was taking place. A few large nymphs were present until September, when only 4 per cent. were in the 9 and 10 mm. classes, while the number in the small classes increased, 78 per cent. being in the 2, 3 and 4 mm. classes.

The growth-rates calculated from these measurements are given in fig. 5. Growth varies from 0·3 to 1·7 mm. per month throughout the year, and shows no obvious relation to the temperature fluctuations of the stream.

The life cycle of *H. lateralis* is apparently univoltine, emergence taking place in this stream in June, July and August. The life cycle does not seem to be as closely inter-related to the temperature as it does in *E. torrentis* and *R. semi-colorata.*

Baetis rhodani (Pictet).

The measurements of the nymphs of *B. rhodani* captured each month from September, 1949, to February, 1951, are given in fig. 7.

In September, 1949, 34 per cent. of the nymphs were in the 2, 3 and 4 mm. classes, 19 per cent. in the 6 and 7 mm. classes, and 22 per cent. in the 9 and 10 mm. classes. The remaining 25 per cent. were scattered between these classes and up to the 12 mm. class. It can be seen from this that three groups
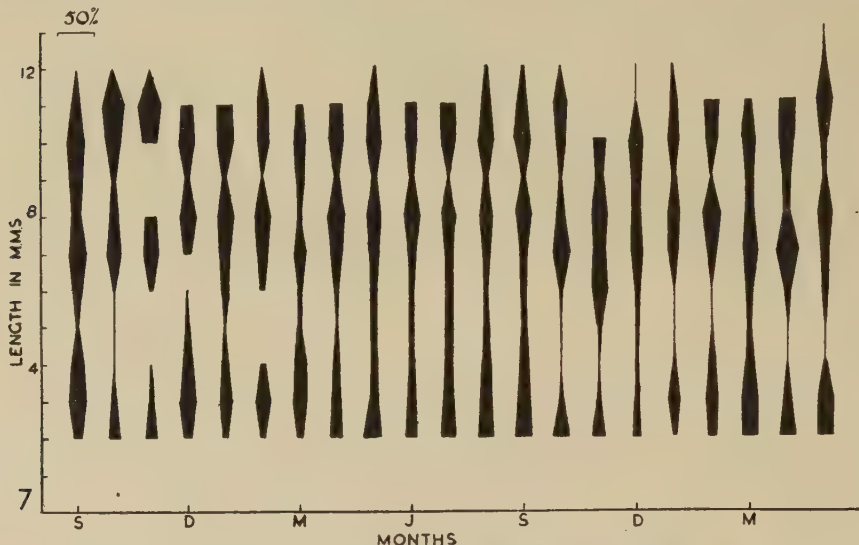
FIG. 7.—The monthly percentage of nymphs of *Baetis rhodani* (Pictet) contained in each millimetre length class.

of nymphs occur. These three groups were present every month till measurements were discontinued, with the greatest concentration of the numbers in the 2–3 mm., 7–8 mm., and 10–11 mm. classes.

Examination of the nymphs showed that there were two size groups of penultimate instar nymphs, one of average length 7 mm., and the other of average length 10 mm.

From the results no indication of the length of the life cycle can be estimated. The presence of the two groups of nymphs ready to emerge, and the presence of all sizes of nymph in all months of the year, makes it impossible to follow the life cycle by measurement alone. Adults were collected in every month of the year except January and February, and the length of the emergence period further complicated any attempt to elucidate the life cycle.

An insufficient number of imagines were collected to show with any certainty whether groupings in size similar to those of the penultimate instar nymphs occurred. It is interesting to note that a similar discontinuous size variation

has been found for an Australian species of the same genus, *Baetis baddamsae* Harker (Harker, 1950).

SUMMARY.

1. The results obtained from the measurements of the lengths of four species of mayfly nymphs each month are described. The species were *Ecdyonurus torrentis* Kimmins, *Rithrogena semicolorata* (Curtis), *Heptagenia lateralis* (Curtis), and *Baetis rhodani* (Pictet).

2. *E. torrentis* was found to have a trivoltine life cycle. The growth-rate varies with the temperature.

3. *R. semicolorata* showed a univoltine life cycle with emergence partly dependent on temperature.

4. *H. lateralis* was found to have a univoltine life cycle. Growth does not show a direct relation to the temperature.

5. The life cycle of *B. rhodani* could not be determined by length measurements. Two size groupings of penultimate instar nymphs were found to be present.

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MOON, H. P., 1939, The Growth of *Caenis horaria, Leptophlebia vespertina* and *L. marginata. Proc. zool. Soc. Lond.* (A) **108** : 507–512.

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BOOK NOTICE.

Caddis. By NORMAN E. HICKIN. 8vo. London (Methuen & Co.), 1952. Pp. x + 50, pls., text illust. Price 9*s.* 6*d.*

This book forms No. 5 of the Field Study Series, the purpose of which is to discuss the problems of the countryside from the intimate angle of the expert but in such a way as to appeal to the general reader, the student, including the older school child, and the teacher.

It is also the first book in English dealing exclusively with the immature stages of Caddis Flies.

The introductory chapter defines the insect and describes special features of its biology, including importance as food for fish and their use in wet and dry fly fishing.

Chapter 2 deals with the life cycle of Caddis and its *Agriotypus* parasite, and Chapter 3 with collecting, rearing and preserving. The morphology of the larva and pupa with keys to the identification of families are dealt with in Chapters 4 and 5.

The final chapter is a guide to research on the biology of Caddis. There are two appendices, one comprising a bibliography of literature on the adult and immature stages and the other a complete list of British Caddis Flies.

The work is very fully illustrated, many of the drawings having previously appeared in the author's series of papers in the Society's *Transactions* and *Proceedings ;* there are also four coloured plates.

LARVAE OF THE BRITISH TRICHOPTERA.—33.

By N. E. HICKIN, Ph.D., F.R.E.S.

Polycentropus flavomaculatus Pictet (Polycentropidae).

THIS most abundant caddis fly is found almost everywhere where moving fresh water is found—not only in streams and rivers, but also on the shores of lakes where there is some wave action.

On 31st July, and again on 6th August, 1951, I found larvae and pupae of this species exceedingly abundant, together with some hatched adults, in the river Breamish about a mile east of Ingram in Northumberland.

The River Breamish was the scene in the late summer of 1949 of very extensive flooding, the violence of which caused the river bed to be scoured out by large boulders, destroying all vegetation in the river and washing away all silt. At the present time the bed of the river is composed only of these boulders, the river flowing swiftly over them. The bed of the wide flood channel is similarly composed of boulders, with more slowly-flowing subsidiary streams running off the main river and running into it again. These side streams were margined with *Mimulus* and other early colonising plants in this otherwise sterile area. Small crustaceans and other animals from the side
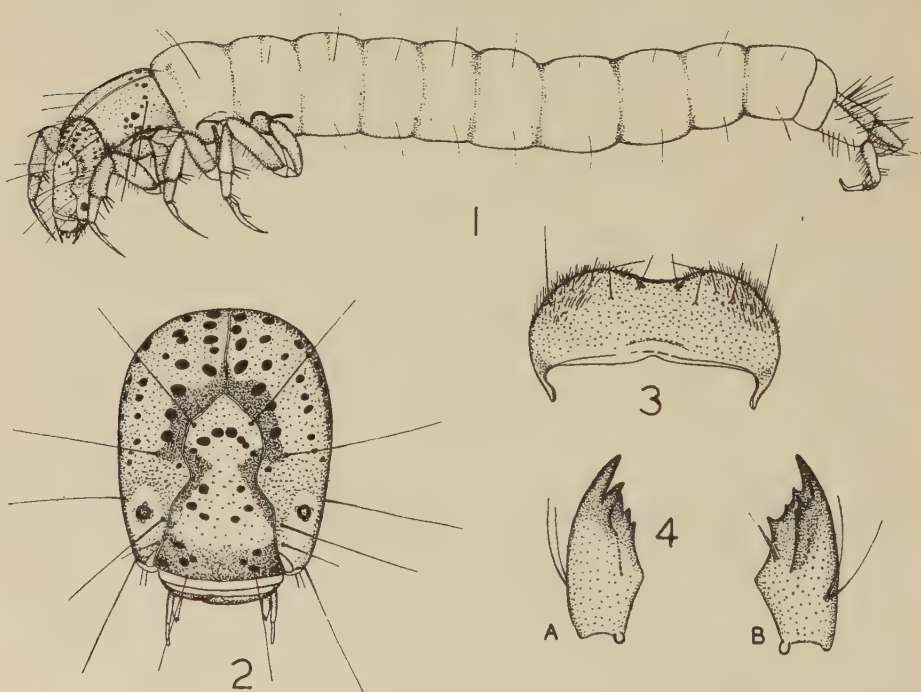
FIGS. 1–4.—*Polycentropus flavomaculatus* Pictet. (1) Lateral view of larva. (2) Head from the front. (3) Labrum. (4) Mandibles. A, right ; B, left, from below.

streams being washed into the main stream were obviously the food of the vast number of carnivorous caddis larvae present in the main stream.

The small silk swallow-nest-shaped nets of the *Polycentropus flavomaculatus* were on the under surface of the large stones and boulders, as were the silken pupal cocoons covered with small stones and pieces of grit. It would be interesting to learn how the larva obtains and carries these particles of stones to the cocoon in the face of the very strong current of water. Larvae and pupae of *Rhyacophila dorsalis* (Curtis) were also extremely abundant, but case-bearing caddis larvae were almost absent. I have to thank Mr. D. E. Kimmins for confirming the identity of these two species, and Dr. E. A. R. Ennion, who introduced me to this most interesting locality.

Larva (fig. 1).—Campodeiform, head probably procentrous but larva is very active and head is often held in orthocentrous position. Thorax and abdomen cylindrical, decreasing in width only slightly towards posterior end and somewhat dorsoventrally flattened. Length 14 mm. This is rather larger than the size given by Ulmer. Width 2 mm. *Head* (fig. 2) elliptical, light yellow in colour, heavily spotted in black (some variation in size and situation of spots) as in figs. 2 and 6 ; in addition a yellowish-brown mark extends within the genae around the aboral end of the clypeus and also within the clypeus around its margin from the constriction extending orally. Eyes situated within a lighter creamy-yellow area. *Gular sclerite* transverse, genal suture long. *Antennae* rudimentary. *Labrum*
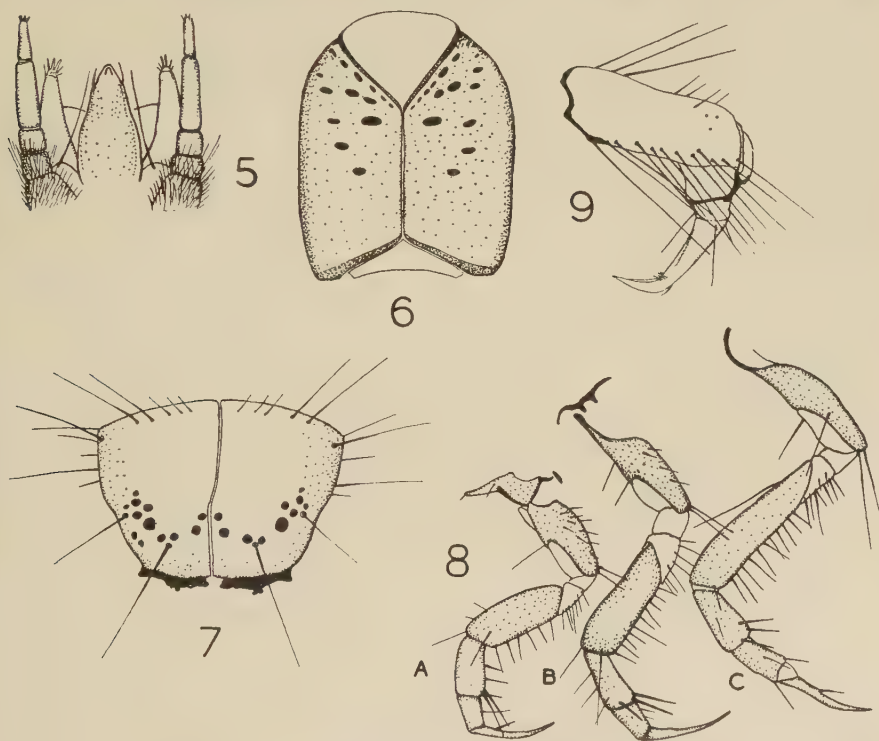
FIGS. 5–9.—*Polycentropus flavomaculatus* Pictet. (5) Maxillae and labium. (6) Head from behind showing gular sclerite. (7) Pronotum. (8) Legs. A, pro-, B, meso-, and C, metathoracic. (9) Anal claw.

(fig. 3) transverse, sclerotised. *Mandible :* Only left mandible has internal brush of hairs (fig. 4). *Maxilla* (fig. 5) : Palp long, four-segmented, third segment much longer than the others. Tips of sense organs at end of galea just reach end of third segment of palp. *Labium* (fig. 5) conical, palps absent. *Thorax :* Pronotum sclerotised, wider anteriorly, light yellow with W-shaped pattern of black spots as in fig. 7 ; posterior margin black, heavily sclerotised. Meso- and metanota not sclerotised. Legs relatively short, differing only slightly in length ; tarsal claws very long but very little curved. Three strong spurs on distal end of each tibia. Prosternal horn absent. *Abdomen :* Colour variable on dorsal surface—reddish brown, buff, yellowish brown or greenish are common. Whitish on ventral surface. Gills absent, lateral line absent. Abdominal segments distinct but not deeply intersected. Anal appendages each of two long segments, with the terminal claw (fig. 9) at right angles to them. The claw is slightly scoop-shaped, with two rows of minute spicules on the inner face terminating distally at a group of somewhat larger spicules. Auxiliary claw present as a sharp bristle, closely adpressed, can be seen only with difficulty. Blunt projection on inner face of tip of claw absent.

SUMMARY.

The larva of *Polycentropus flavomaculatus* Pictet (Polycentropidae) is described in detail and figured.

REFERENCES.

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——, 1909, *Süsswasserfauna Deutschlands* **5–6** : 230.
ROUSSEAU, E., 1921, *Larves et Nymphes Aquatiques des Insectes d'Europe* : 491.
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SILFVENIUS, A. J., 1904, *Acta Soc. Fauna Flora Fennica* **26** : 12.
——, 1906, *Ibid.* **27** : 124.
MACDONALD, W. W., 1950, *Proc. R. ent. Soc. Lond.* (A) **25** : 19.

BOOK NOTICE.

Ecological animal geography. By RICHARD HESSE. Edited by W. C. Allee and Karl P. Schmidt. 2nd edn. 8vo. New York (John Wiley & Sons) and London (Chapman and Hall), 1951. Pp. xiii + 715, text illust. Price 76s.

The first edition of this work appeared in 1937 and was an authorised translation of a famous book by Prof. Hesse published in 1924. While the character of the original edition is maintained, the incorporation of the results of fourteen years further research and study have resulted in an essentially new work. The major revisions provide (1) a greatly simplified terminology, (2) a suitable background for modern interest in conservation on a world wide scale, (3) expansion and revision of a large amount of material, and (4) expanded chapter bibliographies, including relevant recent publications.

In its present form the book comprises 28 chapters and an index, the chapters being grouped under the following four headings, (1) the ecological foundations of zoogeography, (2) the distribution of marine animals, (3) the distribution of animals in inland waters, a phase of limnology, and (4) the distribution of land animals.

LARVAE OF THE BRITISH TRICHOPTERA.—34.

By N. E. HICKIN, Ph.D., F.R.E.S.

Tinodes assimilis McLachlan (Psychomyidae).

THE adult fly of this species has, for a long time, been associated with waterfalls and rock springs. Its larva was, however, unknown. I am, therefore, very
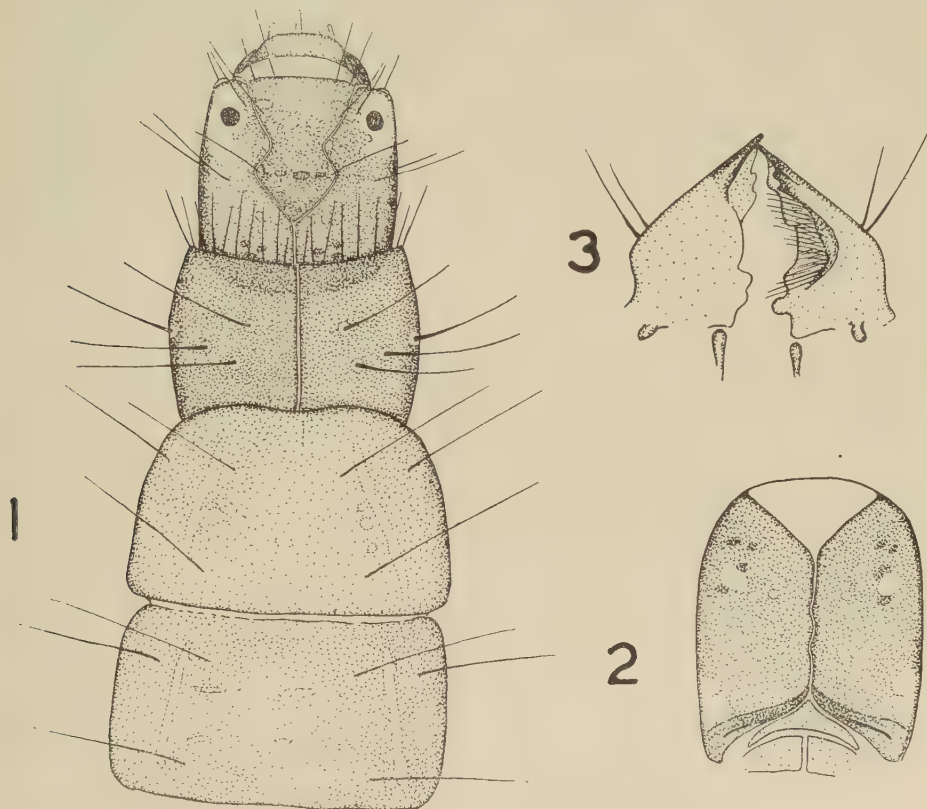
FIGS. 1–3.—*Tinodes assimilis* McLachlan. (1) Head and thorax of larva. (2) Head of larva from beneath. (3) Mandibles of larva from beneath.

grateful to Dr. E. J. Popham, who kindly gave me some larvae of this species which he had collected from Braddon Head, Port Erin, Isle of Man, on 24th March, 1951. Mr. W. D. Hincks had originally collected an adult from this locality on 23rd March, 1950, which was identified by Mr. Henry Whitehead.[1]

[1] Since writing the above I collected a number of the larvae of *Tinodes assimilis* McL. on about four square feet of wet rock surrounded by pavements and brick walls in the centre of Tramore, Co. Waterford, Ireland, on 12th June, 1952.

This record is the first for Ireland, and I am grateful to Miss Geraldine Roche of the National Museum of Ireland for searching the Irish National Collections for this species.

The long fixed galleries are very similar to those already described for the species of the family Psychomyidae. They are about 5 to 6 cm. in length and 3 to 4 mm. wide. composed of silk to which detritus is attached, and occupy irregularities in the rock surfaces over which a thin film of water is running. The pupal cocoon is built within the larval gallery. Dr. E. J. Popham has made a study of the fauna associated with thin films of water running over vertical rock surfaces—the *Fauna Hygropetrica*—in which, in certain conditions, *Tinodes assimilis* larvae play an important part.

Larva.—Campodeiform, head procentrous. Head and pronotum dark greyish-brown, rest of body dark greyish-brown gradually turning to light chestnut-brown towards the hinder end. Length 8 mm., width 1·5 mm. The larva closely resembles that of *Tinodes pallidula* McLachlan, and in this description only points of difference between them will be discussed. *Head* (fig. 1) : Dark greyish-brown except for patch around eyes, light yellowish-brown. Four pairs of small light marks on the clypeus and genae (the central constriction of the clypeus), as in fig. 1. On ventral surface of head the dark greyish colour reaches anterior margin of genae, except for patch in region of eyes. The fold at the anterior margin of genae on the ventral surface much wider than in *Tinodes pallidula*. Labrum golden brown. Teeth of mandibles sharper than in *Tinodes pallidula* (fig. 3). Antennae somewhat larger and antennal bristle more prominent than in *Tinodes pallidula*. Pronotum slightly darker than the head. *Legs :* Prothoracic legs slightly larger and more robust than meso- and meta-thoracic legs.

SUMMARY.

The larva of *Tinodes assimilis* McLachlan (Psychomyidae) is described in detail and figured.

REFERENCES.

HICKIN, N. E., 1950, *Proc. R. ent. Soc. Lond.* (A) **25** : 103.
MOSELY, M. E., 1939, *The British Caddis Flies* (*Trichoptera*). London.
POPHAM, E. J., 1951, *Proc. R. ent. Soc. Lond.* (C) **16** : 48.

THE GROWTH OF THE HEAD CAPSULE AND ANTENNAE OF *ANISOLABIS LITTOREA* (WHITE) (DERMAPTERA : LABIDURIDAE).

By E. T. GILES, M.Sc., F.R.E.S.

INTRODUCTION.

A. littorea is an earwig endemic to New Zealand and the off-shore islands, of common occurrence in damp beach wrack above the reach of tides. The present paper is based upon a consideration of nearly 300 nymphs and adults collected in the vicinity of Auckland.

During development *A. littorea*, as shown from breeding experiments (Giles, 1952), passes through five nymphal instars, none of which exhibit sexual dimorphism externally. Owing to the telescopic nature of the abdomen, the body length is not a completely reliable measurement for developmental studies and is useful only as a guide to size ; nor would it be an adequate systematic character. This must apply to other species of Dermaptera, and it seems that body lengths given by authors should be taken as only relative. The precise separation of the instars of *A. littorea* is the subject of the present paper.

For other species of Dermaptera head capsule growth has been considered by Henson (1947) and antennal growth by Meinert (1864), Terry (1905, 1906), Chapman (1917), Crumb, Eide and Bonn (1941), Lhoste (1942), Henson (1947) and Hincks (1948). The results of these workers would appear to have been based on very much smaller numbers of specimens than used here. *Forficula auricularia* L. was most commonly studied and there is some variation in the results of the different authors.

ACKNOWLEDGMENTS.

THE GROWTH OF THE HEAD CAPSULE.

The mean head widths (taken at the broadest part behind the eyes), together with other relevant data concerning each instar, are given in Table I.

TABLE I.—*The head capsule width of the instars of* A. littorea (*in units of* 0·1 mm.).

Instar.	Observed range.	Calculated range.	Number.	Mean.	σ.	V.	Growth ratio.
I	11·6–13·2	11·1–13·5	57	12·3±0·05325	0·4020	3·268	
II	12·8–15·2	12·8–16·3	35	14·6±0·09333	0·5521	3·612	1·19
III	16·0–18·4	15·7–19·3	54	17·5±0·08370	0·6151	3·515	1·20
IV	20·0–22·0	19·3–23·3	31	21·3±0·1804	0·6506	3·054	1·22
V	22·4–28·9	20·1–30·9	28	25·5±0·03397	1·798	7·193	1·20
♂	26·4–35·1	25·2–38·8	32	32·0±0·4960	2·268	7·087	1·26
♀	26·4–40·4	22·5–43·7	45	32·6±0·5030	3·375	10·35	1·28

Total . . . 282

Overlapping of the observed ranges occurs twice, namely between the first and second instars and between the fifth and adult, but in the calculated range all stages overlap. This condition is in line with that found in *F. auricularia* by Henson (1947).

In the majority of cases the head capsule width provides a means for the determination of the nymphal instars of *A. littorea*. Consideration of the antennae enables first and second stages to be separated. Fifth instar nymphs and adults can always be distinguished, as the abdomen of the former possesses ten terga whereas that of the female has but eight and the male's unequal forceps mark it immediately. Should specimens be encountered in the overlapping portions of the ranges of other nymphal instars, then the antennae, as shown in the consideration of their growth, would almost certainly allow of a separation being made.

The differences between the mean head widths of successive instars show a high statistical significance. None, however, is exhibited between the means of the males and the females—in contrast to the condition in *F. auricularia* (Henson, 1947). The difference between the two means is only 0·95 times its standard error and a *t* test applied to them gives $P > 0.9$. The mean head widths of the instars of *A. littorea* were submitted to the same analysis as applied by Henson to *F. auricularia*, so that a comparison between the two species might readily be made.

It is apparent from a consideration of the growth ratios that every instar is represented. It is now known that these ratios are rarely constant, and the longer the stadium the greater the amount of growth (Richards, 1949). This is in agreement with the longer duration of the fifth instar of *A. littorea* as given by the tentative figures of Giles (1952) (47 days as against 23–36 days for other instars). Henson's results show that *F. auricularia*, on the other hand, exhibits a reduction in the growth ratio between fifth instar and adult compared with that between nymphal instars. No data on the length of the stadia of this species are given, but the drop is held to be associated with the effect of the growth hormones.

The Growth of the Antennae.

The antennae of *A. littorea* are of the annulate type of Imms (1940) and in both nymphs and adults consist of a long scape freely movable on the antennifer, a very short pedicel and a flagellum which increases in length with each moult (fig. 1). The proximal annulus of the flagellum—the "so-called 'third segment' or second annulus" of Imms (1940), the "article de croissance" of Lhoste (1942) and the "meriston" of Henson (1947)—is very long, and, in fact, always the longest segment of the flagellum. The term "meriston" will be used here to denote this annulus, by the division of which the growth of the antenna is brought about; but the third segment of the adult antenna cannot be so designated.

In nymphs of *A. littorea* which exhibit signs of being about to moult, it is possible to distinguish within the meriston the incipient segments of the next stage (fig. 1g). Growth of this segment is recorded for *F. auricularia* (Lhoste, 1942, and Henson, 1947) and for *Chelisoches morio* (Fabricius) (Terry, 1905). Lhoste and Henson both figure the meriston of *F. auricularia* as having shallow
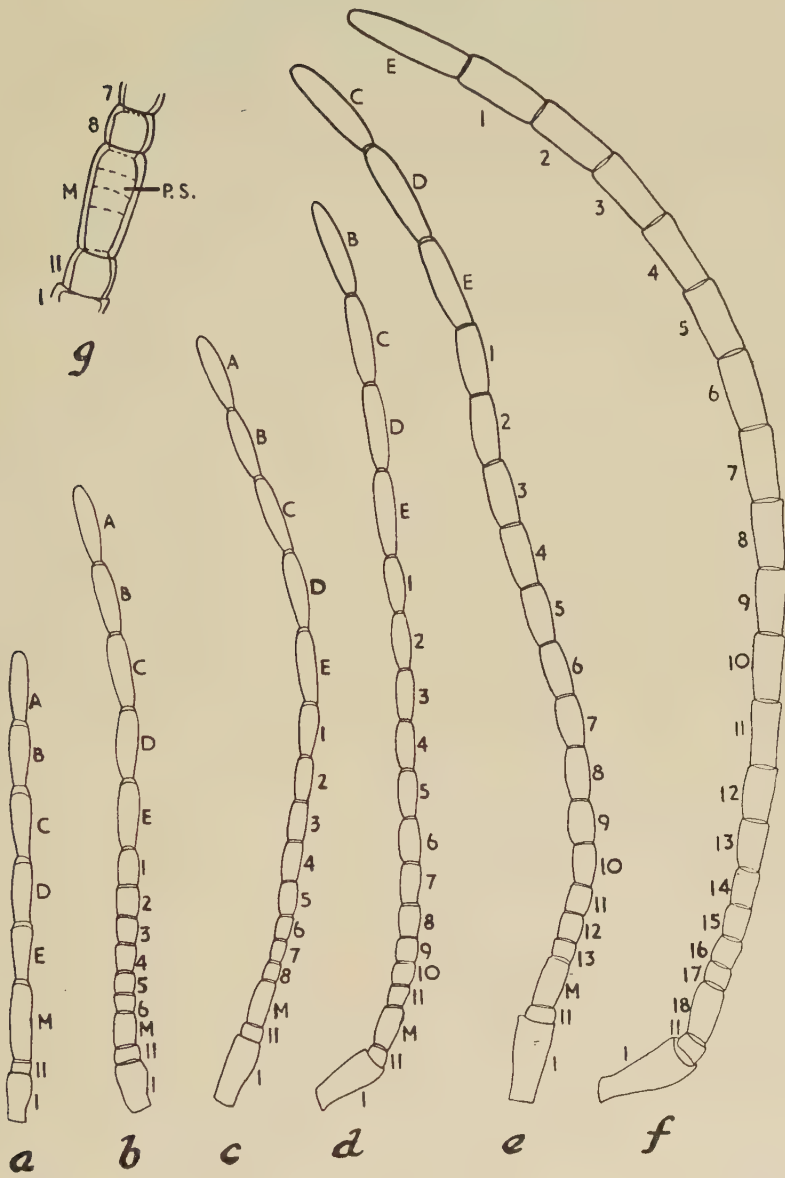
FIG. 1.—Antennae of the instars of *A. littorea*, portion of the scape of each missing
(a–f × 14; g × 32). a–f, typical antennae of the instars arranged in order;
g, basal portion of antenna of a third instar nymph about to moult; I, scape;
II, pedicel; M, meriston; 1–18, annuli of the middle region; A–E, annuli of the
apical region; P.S., preformed segments.

external grooves, the former author indicating in his figure that these are the sites of later divisions of the segment. In *A. littorea*, however, the meriston is quite smooth and there is no sign externally of future partition.

Comparison of the antennae of successive instars of *A. littorea* reveals the distinctness of certain portions throughout life. First stage antennae consist of a scape, a pedicel and a meriston succeeded by five fairly long annuli (fig. 1*a*); in the second instar there is the scape and pedicel, but the meriston is followed by a group of five or six very short segments succeeded by five long ones (fig. 1*b*). The group of short annuli results from the division of the meriston and the terminal series is referable to the distal group of five in the first instar. Antennae of later stages follow the same plan with increasing numbers of short segments in the flagellum (fig. 1*c–f*). The reduction in the number of long annuli which occurs in later instars is dealt with below (p. 95).

In consequence of the distinctness of the groups of annuli the antennae are here divided into three regions : the scape and pedical comprise the " basal region," the meriston and the short annuli resulting from its division constitute the " middle region," and the long distal segments (the representatives of the five from the first instar) make up the " apical region." In *F. auricularia* Henson's figures would seem to show that the apical region remains distinguishable, at least for the second and third instars, and Lhoste's drawings of portions of the antennae of the same species tend to confirm this for the second instar. But the distinction is not as marked as is the case in *A. littorea*.

The system which Henson (1947) discusses for the numbering of antennal segments has the very great advantage that the one annulus bears the same number throughout all instars. This is adopted but extended here so that, in addition, the identity of the three regions may be retained. Roman numerals are used for the basal annuli : I for the scape and II for the pedicel. Arabic numerals, commencing distally, are employed for the middle segments, except that M designates the nymphal meriston. Roman capitals, commencing distally also, are used for the apical annuli (fig. 1).

The number of divisions of the meriston is variable, both within an instar and between the stages, as shown by Table II, which is based upon counts on antennae having apical segments present. In the later stadia this variability is greater than in the earlier, which may be expected in view of the cumulative effect of variation. Both antennae of a specimen do not necessarily have the same number of middle annuli.

The segment count in the middle region is, though variable and sometimes common to two stadia, a guide for determining an instar, and would be particularly useful if the head width of a specimen fell in the overlapping portion of the ranges of two stages. If these two criteria together left the determination of the stage of development in doubt, the general body length would have to be considered.

Progressive loss of apical annuli during life is the rule, the extent of which is shown in Table III. This is only to be expected of a carnivorous insect living in close communities under beach debris and having a life cycle of at least 1½ years. When specimens were kept in the laboratory during the course of the work the damage was greatly accelerated, as a result, no doubt, of the close association of many individuals in small containers.

TABLE II.—*Number of annuli in the middle region of the antennae of nymphs and adults of* A. littorea.

Instar.	Number of antennae.	Number of annuli.	Frequency.	Increase.*
I	114	1	114	
II	70	6	21	
		7	49	5–6
III	101	9	56	
		10	41	
		11	4	3–4
IV	52	11	8	
		12	31	
		13	13	2
V	38	13	3	
		14	16	
		15	13	
		16	6	2–3
Adult	44	16	7	
		17	6	
		18	12	
		19	15†	
		20	4†	3–4

* The lower figure is obtained by taking the difference between the lowest number of annuli of one instar and that of the preceding instar ; similarly the higher figure is the difference between the greatest numbers of segments. All methods of estimating the increase from the data must be liable to error, but this probably gives a result very close to the true value.

† These are dealt with more fully in the consideration of the antennae of adults (p. 96).

TABLE III.—*Percentage frequency of annuli in the apical region of the antennae of* A. littorea.

Instar.	Numbers of apical annuli.*						
	5	4	3	2	1	0	
I	81	13	5	1	.	.	Percentage frequency
II	71	13	8	6	2	.	
III	35	32	14	8	5	6	
IV	.	35	18	14	14	19	
V	.	4	31	21	9	35	
Adult	.	.	.	2	18	80	

* In all cases where there were fewer than five, a terminal scar showed this reduced number to be due to annuli breaking off.

Table IV gives an analysis of the frequencies of the total numbers of antennal annuli at all stages. The range in each stadium is due both to the variability in the division of the meriston and to the damage suffered by the antennae during life, and is greater in the later instars than in the earlier.

It will be readily appreciated that in *A. littorea* the total number of antennal annuli cannot be used with reliance for developmental or systematic studies.

TABLE IV.—*Frequencies of the total numbers of antennal segments of* A. littorea.

Instar.	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	Total.
I	5	1	2	8	15	83*															114
II						1	1		2		1	10	8	10*	37*						70
III						1	1		2	2	4	6	12	28	14	24*	14*				108
IV										1	1	2	3	5	5	7	13	18	7		62
V											1	3	4	4	3	4	6	8	18	5	56
Adult			2	3	3	5		4	5	4	7	6	8	9	16	10	21	17	29	5	154

* Indicates undamaged antennae.

Previous workers on the Dermaptera have recorded antennal segment counts, but the species considered show little variation in this respect at any stage of development. This constancy could be due to the consideration of a small number of specimens, or to less damage being suffered by the antennae during life, or to the absence of variability in the growth of the antennae.

The antennae of adults.

In adults the antennae are equal to about half the body length. The three regions of the nymphal antenna are discernible, although the boundary between the middle and apical groups is not as sharply defined as in the nymphs. It was found that the adjacent segments of the two regions had lengths in the ratio 1 : 1·4. Counts of the antennal annuli of seventy-seven recently captured adults showed that only twenty-two of them bore antennae with members of the apical group present ; eight had one or two on both antennae, and fourteen one on but one of them.

Table V shows the results of counts on these antennae which had apical annuli present, giving reliable evidence of the composition of the adult antenna.

TABLE V.—*Adult antennae of* A. littorea *on which apical members present.*

Number of annuli in middle group.	Number of antennae.
16	7
17	7
18	14
19	2

Although antennae lacking apical segments cannot give satisfactory information about the number of middle annuli, the results of counts given in Table VI should be considered.

TABLE VI.—*Adult antennae of* A. littorea *on which apical members absent.*

Number of remaining middle annuli.	Number of antennae.
19	13
20	4

This table shows the maximum number of middle annuli in the present sample to be twenty. It is possible that, as these were on antennae lacking

apical members, some may be found with more than twenty. Another aspect is that antennae with nineteen middle segments are more common than Table V would indicate. These, also, may have originally possessed more than nineteen. The data of Table VI show that higher numbers of middle annuli occur than is indicated by Table V. As a result an upward tendency is given to the number of middle segments of the adult antenna.

It is apparent that the number of segments which should compose an adult antenna of *A. littorea* cannot be stated with any degree of accuracy, and is certainly not a reliable systematic character as used by White (1846) in his original description of the species.

It seems to the writer that in the Dermaptera, a notably difficult group taxonomically, the head capsule width and the detailed structure of the antennae might be used with advantage for systematic purposes. The head width would be a far more reliable guide to the separation of the instars than the numbers of antennal segments, if the variation of *A. littorea* in this respect is present in other species. Should the middle region of the antennae be readily distinguishable, then this portion would be of much greater use than the whole organ. The writer considers that the two basal segments of the antenna would be relatively constant and unaffected by the variability of the remainder and that, therefore, their lengths could be usefully included in systematic descriptions.

Summary.

1. During development *A. littorea* passes through six instars—five nymphal and the adult.

2. The means of the head widths of successive instars show a growth ratio which is very nearly constant.

3. For the very great majority of specimens the head capsule width provides a means of separating instars, but where overlapping of successive stadia occurs recourse must be made to the antennae.

4. Growth of the antennae takes place by means of the division of the meriston (the first segment of the flagellum), but this growth is variable not only within an instar, but also between the stadia.

5. The antennae of all instars are separable into three regions. A method of numbering these parts is given so that the identity of each is retained and each segment keeps the same number throughout life. The middle region is the most useful for determining an instar.

6. Progressive damage and loss of terminal antennal segments occurs during life, with the result that counts involving all annuli are not reliable.

7. Suggestions are made for the use of the head capsule width and the detailed structure of the antennae in dermapteran systematics.

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* Not seen in original ; quoted from Terry (1906).

SOME PROBLEMS OF POLYMORPHISM IN INSECTS.

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Introduction.

The success of insects as an animal group has been attributed to their enormous capacity for reproduction, coupled with a flexibility of form which has resulted in endless adaptations to environment. Insects have existed as a distinct group for so long a period in the earth's history that it may not be so immediately apparent that this process of selective adaptation is still continuing on a very wide scale at the present time. Indeed were it not so, their extinction on the same scale of time would not be far off.

However, the forces of natural selection exert their influence not only on a set series of insect types, but on the variety of patterns produced within those types. It is this large range of variation that is coming more and more into prominence through the accumulation of recorded observations. As the variants of a particular form must ultimately play such an important part in the perpetuation of that form, it is obvious that a better understanding of the mechanism of their production can provide a basis for the study of their ecology. In order to approach this problem of insect polymorphism, it is proposed to refer to a series of publications on variation which reveal some of the principles involved.

The Genetic Basis of Variation.

Races and Variation.

The concept of a species has been shown in an increasing number of cases to apply to a series of closely allied variants rather than one particular form of individual. In some species the constancy of the features of the variants has led to the identification of specific sub-species and races, while in others confused lists of variations are available with no clear indication as to whether the variants are genetically controlled races or have resulted from some environmentally modified factor. An approach could be made by considering some of the aspects of race differences and the form of ecological distinction to which they lead.

Perhaps the most conspicuous factor in the incidence of polymorphism in insects is colour. Numerous species of Lepidoptera have been shown to have distinct colour races, such as the yellow and orange races of *Colias chrysotheme* Esper (Pieridae). There is good reason to regard many constant morphological variants in insect species as distinct races after the Law of Homologous Series (Vavilov, 1922). By the study of variants in closely allied species or genera this provides some criteria for the degree of variation that may be expected. This view was taken by Rubtzov (1935) in analysing the form of variation existing in certain species of the non-swarming grasshoppers of the genus *Chorthippus* and others. He found parallel series of naturally occurring colour

forms which showed their genetic basis by breeding true to their colour type irrespective of the environment, and which therefore could be regarded as genetic races. On the same basis, Dobzhansky (1933), showing a similar parallelism in the variability of related species and genera of the Coccinellidae, goes on to state that such homologous varieties of different species may be more similar to each other in appearance than different varieties of the same species. He attributes this genotypical parallelism to a probable essential similarity of the germ plasms. Clark (1943), on the other hand, deliberately avoids these considerations, and restricts himself to a purely descriptive method of the colour variation in British Acrididae.

Perhaps one of the most striking phenomena associated with polymorphism is that of "mimicry" in butterflies and a few of the day-flying moths. This phenomenon occurs chiefly in the tropics, and we find that the wing pattern and colour of the "mimic" may bear an extraordinary likeness to that of the "model." The mimicking forms are frequently restricted to the female sex, though sometimes both sexes or only the males are concerned. The mimics are generally less abundant than the models, but they usually involve a greater number of species. The capacity of a mimicking species to produce a number of polymorphic forms is remarkable. Thus the Swallow-tail (*Papilio dardanus cenea* Stoll.) produces at least thirteen distinct adult forms. Of these, ten occur in the female sex which, having no " tails " to their wings, mimic non-Swallow-tail models. However, it is interesting to note in such cases that the models are closely related. Punnett (1915), in his concise book on mimicry, suggests a genetic background which produces parallel combinations of gene characters in both the model and the mimic.

Variation within a species of the types described above is to be contrasted with variation caused by hybridization. For example, although the number of spots in any given species of Coccinellid is genetically controlled (Dauguet, 1949), Bauer and Timoféeff-Ressovsky (1942) illustrate the crossing of a Corfu race of *Epilachna chrysomelina* Fab. with a dark Egyptian race to produce 24 distinct variations of dark colouring and black flecks.

Although other features, such as size, may be associated with colour variation between races, the differences are seldom purely morphological, but are extended to include both aspects of physiology and behaviour. Thus Rubtzov (1935) showed that the green forms of the grasshoppers were not only larger than the brown forms, but were more mesophilous. Hovanitz (1944) states that in the case of *Colias chrysotheme*, the orange race has extended with regions growing alfalfa in North America, whereas the yellow race has remained in regions of red and white clovers. This occupation by the orange race has been accompanied by a genetic acclimatization selection or by intercrossing with the yellow race, as a result of which the recently migrant orange race has now become resident. Further, probably due to its ability to undergo winter diapause, the yellow race has a greater range north and south. Thus a different genetic potentiality for winter hibernation, food-plant and environmental preference has provided the basis for the formation of geographical races.

A similar geographical division is taking place in N. America in the case of the European Cornborer (*Pyrausta nubilalis* Hübner), in which there are two races, an unimportant univoltine race, and a bivoltine race which is spreading west with agriculture and becoming an increasing pest. Thus small racial

differences as determined by the genetic constitution, can lead by progressive environmental changes which favour one form, as occasioned, for example, by agriculture, to the establishment of a future geographical race. On a larger scale Dobzhansky (1933) finds the geographic variation of lady-birds (Coccinellidae) to be in accordance with Allen's rule, in that there is depigmentation in arid regions and an accumulation of pigment in humid regions, so that he is able to specify widely separated centres of light-coloured forms, with a general increase in the development of dark pigmentation the further the specimen is from the centres. Since most available evidence points to a hereditary factor in such colour variation, Dobzhansky agrees with the conclusion of Timoféeff-Ressovsky (1932) that gene complexes as epitomised in the occurrence of parallel races may, under given geographical conditions, exert a selective influence.

Sexual Dimorphism, etc.

The genetic constitution can also lead to a much more specific form of individual variation in such phenomena as sexual polymorphism. It is probably most distinctly represented in the social insects, but is also of wide occurrence and is diverse in form. Sexual differences may appear in the wing colour pattern, as in many species of the Pieridae ; or in structural formations, as in the general body size, and the size and shape of various parts and appendages, such as the anal cerci in earwigs, the mandibles in stag beetles, the more pectinate antennae and smaller size of the male imago of the Emperor Moth (*Saturnia pavonia* L.). Such dimorphism is associated with dominant sex-linked genes. When the sex-linked factor, however, is a recessive, variants may be produced, as in the case of *Abraxas grossulariata* L., where a rare light form, *A. lacticolor*, is found in nature only as a female (Crew, 1933).

THE ENVIRONMENTAL BASIS OF VARIATION.

Geographical Variation.

It is inevitable that geographical variants are the result of the genetical constitution and of the environmental influence which may not be evidentially separable. Thus Johnson (1939) showed for the Bed Bug (*Cimex lectularius* L.) a positive correlation between head width and latitude in the N. hemisphere, due apparently to the combination of the genetic potentiality and the optimal growth temperature. Tutt (1902) inferred that there was some evidence for geographical variation of *Saturnia pavonia* within Great Britain, and certainly between the native form and those from S. Europe, which are larger and brighter and more thickly scaled. This variation is attributed, at least in part, to environmental conditions, on the grounds that the longer the pupal diapause the paler the colour, and that differing developmental temperatures may artificially induce autumn emergence or postpone the spring emergence, and so lead to thin scaling. On the other hand, there may be a genetical factor influencing the geographical variant in the same direction, as with pigment accumulation in lady-birds. The border colour pattern of *Colias chrysotheme* may be augmented by high humidity, but it is also augmented by intensive interbreeding between the yellow and orange races, so that the border pattern is reduced in areas where the two races do not overlap, as in Eastern U.S.A., where the reduction is greatest (Hovanitz, 1945). Geographical variation,

therefore, can be expected to be very diverse in nature due to the wide range of influences involved.

Seasonal and Climatic Variation.

In many ways the factors involved are rather similar to those concerned with geographical variation. The wing pattern in *Colias chrysotheme*, for example, is reduced when exposed to autumn, winter and spring climate, and is only fully developed in the summer generation (Hovanitz, 1945). As with the geographical variant, the seasonal variant depends on the extremes experienced and the genetic strain. A contrasting example exists in the Colorado beetle, *Leptinotarsa decemlineata* (Say), where the more unfavourable seasons of autumn winter and spring are associated with the production of a long-winged migratory form, whereas the summer form is short-winged (Klingstedt, 1939).

Although it would appear that temperature plays an important part in the production of seasonal variations, other aspects, such as length of daylight, must exert an equivalent influence. In aphid forms it is thought that long days are responsible for the production of viviparous parthenogenetic forms in summer, while short days result in oviparous sexually fertile forms.

In the ladybird, *Adalia bipunctata* L., there are two allelomorphs ; one is red with two black spots, and the other black with two red spots. Timoféeff-Ressovsky (1940) showed that a seasonal variation occurs in the relative frequencies of these two forms from a minimum of 40 per cent. of the red form in the autumn to a maximum of 70 per cent. in the spring. He considers that the relative frequency of the red form is favoured by a lower survival rate of the black form during winter hibernation. The species has at least two generations per year, and it is suggested that a greater fertility and developmental vitality in the black form leads to a reduction of the relative frequency of the red form by the autumn.

Nutritional Effects.

Many observations have been made which have led various authors to attribute colour variations in the larval state, at least in part, to the differing food material of the individuals concerned. Quaintance (1905), referring to the cotton bollworm (*Heliothis obsoleta* (Fab.)), states that larvae feeding on cotton are a pale pink or green, whilst those on alfalfa are of a more uniform green type. A similar type of observation was made by Cockayne (1930), with the related species of *Heliothis peltigera* Schiff., in that larvae feeding on *Convolvulus soldanella*, in which the flower has a pink-striped petal, were mostly pink, whilst those on *Senecio* at the same time were mostly green. Thus, whatever further effects result from differing food-plants, there would seem to be a parallel in other species for the generalisation of Sevastopulo (1943), in stating that Pyralid larvae are yellow or reddish when feeding on flowers, but green when on leaves. However, the problem still exists as to the principles involved ; is the observed colour variation a product of differing metabolism or directly related to the plant pigment, or a derivative thereof, or is it nothing directly concerning nutrition but a part of the insect-plant relationship, in which there is a physiological response to the plant colour only in so far as it forms a part of the background environment ? Although Poulton, as long ago as 1886, considered

such insect-plant relationships in relation to the effect of natural selection, relatively little work has since been done to determine whether different food materials involve a simple metabolic response, or an individual physiological response. Thus, at present we are quite unable to explain the type of variation such as that of *Sphinx ligustri* L., where larvae fed on ash or lilac are darker than those fed on privet (Poulton, *cited in* Tutt, 1902), or of *Cerura vinula* L., which develops a pale grey-green saddle when feeding on aspen instead of the usual chocolate brown (Sevastopulo, 1943). In the case of certain lepidopterous larvae and other insect forms the gut contents are visible through the surface cuticle, and naturally the colour of the food material will influence the overall colour of the insect so that different coloured foodstuffs will produce apparent colour variants.

A singular example of a colour basis which could lead to colour variants, and perhaps be attributable to a nutritional aspect, lies in the relationship which Mahdihassan (1946) showed to exist between the colour of certain scale insects and the pigments produced by their symbiont bacteria. This is certainly an aspect of investigation which might well be extended to other forms.

On the relationship between nutrition and insect size, Chapman (1931) states that the Bean Weevil may develop into adults 8 per cent. of the normal size[1] if the larvae are restricted to a small portion of the bean. Hunter and Pierce (1912 : 35–36) attribute the small dimensions of adult Mexican Cotton Boll Weevils reared from small cotton squares to the relatively small supply of available larval food and the short period of larval development. It would seem therefore that (although Goetsch (1924) found, in the case of aquatic planaria and tadpoles, that the less the living space the smaller the size of the growing animal) in the insects the nutrition in the developmental period is the conditioning factor of the ultimate adult size.

Basu (1943) attempted a fundamental approach by studying the effect of some 20 different plant foods on the larval and post-larval development of *Prodenia litura* Fab. He found that some plants, such as lettuce, resulted in a short period for larval and pupal development, while others, such as cotton leaves or cabbage, led to a long period of development and small insects. However, the author does not consider an insect-plant relationship, and does little to explain the nature of the nutritional variation. The whole of the nutritional aspect is probably more directly related to the older simple observation of Herms (1907, *cited by* Chapman, 1931) on the flesh fly, *Lucilia caesar* L., that the size obtained is proportional to the number of feeding hours. Thus, whether the insect-plant relationship results either nutritionally or more indirectly via a physiological response in form variations, such an insect-plant relationship must exist and its form must affect the ultimate level of nutrition of the insect, and so influence characters depending directly thereon.

Environmental Background.

The form of the adult insect is as a rule subject to little alteration once it is attained, so that it is natural that most of the observations on the effect of environment in producing variation should concern the period of development

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[1] The basis for the determination of size is not given in the text, but presumably is by weight.

only, and that relatively little is known of the effect, if any, of the environment of the adult.

Much attention has been given to the aspect of the relationship between insect colour and that of its background.   In early investigations Gould (1892) showed a simulatory colour response by breeding from the same batch of eggs two sets of the larvae of *Rumia luteolata* (L.) (*crataegata*) in green and dark surroundings respectively, while Tutt (1899) gives a list of species of the genus *Catocala* which give a similar larval response, and other species which are highly sensitive to the background coloration.   However, little is added to the work of Poulton published in a series of papers from 1885 to 1893, in which he considered the stimulatory effect of the predominant food-plant colour (1886). From the aspect of direct response to colour Poulton (1892) showed some evidence in certain lepidopterous larvae, and sometimes their pupae, for colour simulation, where backgrounds of yellow-green, yellow, orange or white may evoke green, while blue-green, blue, deep red, brown or black may result in dark larvae or pupae.   However, such variations, produced in the larval condition, do not appear ultimately to affect the adult form.   More recently a similar response has been shown by Faure (1932), this time in the Orthoptera.   By breeding *Locustana pardalina* (Wlk.) and *Locusta migratoria* (R. & F.) in painted boxes, he found that the majority gave a simulatory response against backgrounds of white, black, grey, yellow and brown.   He found no colour semblance to green, pink or blue backgrounds.   Green hoppers must be the result of a totally different type of response and we find they are produced in a moist atmosphere with an abundance of succulent food.

This reaction to background colour has naturally led to a study of the effect of light wave-length.   Poulton (1892) himself began this by using coloured filters, but did not obtain results which strictly accorded with his previous findings.   Brecher (1925) suggests that the incidence of white, green or dark brown pupae of *Pieris brassicae* (L.) depends on the wave-length of the light entering the eye of the pupating larva.   Hertz and Imms (1937), in studying the colour response of *Locustana pardalina* and *Locusta migratoria* as observed by Faure (1932), did not obtain so complete an adaptation.   They found that the colours affected were black and orange-yellow.   A background reflecting a large proportion of the yellow rays between 5500 and 6000 Å will stimulate the production of orange-yellow pigment.   But if these rays are replaced by wave-lengths at the blue end of the spectrum below 5000 Å, the resulting insect is a somewhat colourless pale grey which becomes darker when the shorter wave-lengths are reduced.   In general, wave-lengths greater than 6000 Å induce the production of a dark brown pigment.   This form of response applies where the incident rays are ordinarily mixed with daylight, which thereby affords a contrast with the reflected light.   Hertz and Imms then suggest that this may operate through the upper and lower regions of the eye to affect an ultimate hormonal regulation of the pigment, as has been shown to exist in the Phasmidae. This conception of light contrast may explain why Poulton (1892) obtained results with coloured screens which did not agree with those obtained with daylight against coloured backgrounds, and why Grayson (1942) found no effect of coloured light on *Melanoplus bivittatus* Say, as under the conditions of the experiment no such contrast existed.

However, in all this there is one aspect not yet fully considered, and that is

the effect of absence of light. Poulton found that it could result in the production of dark forms, but stated (1892) that it did not produce so great an effect as strong light on black surroundings. Sevastopulo (1946) attributes a dark larval Danaid and possibly also a dark larva of *Cosmophila fulvida* Guenée (Noctuidae) to lack of bright light. Fearnehough (1947, 1948), in the cases *Papilio machaon* L. and *Euphydryas aurinia* Rott., obtained dark pupae from larvae which pupated in complete darkness and green pupae from those in light, though Sevastopulo (1947), using pupating larvae of *Papilio polytes* L. and *P. demoleus* L., did not obtain a comparable result, and inclines to a view relating pupal colour with the amount of late larval movement. Further, although certain locusts may produce dark forms when bred in darkness, Grayson (1942) found no effect was produced on the grasshopper *Melanoplus bivittatus*.

However, as on the one hand bright light on a black background which would afford a maximum contrast, and on the other hand an absence of light and naturally all contrast, may both result in the production of dark forms, it would seem improbable that this is a simple simulatory response, particularly as many insect and other forms which habitually live in the complete absence of light, in such habitats as caves, show a complete absence of pigment.

Larval Population Densities and the Incidence of Phase.

Further considerations of the effect of the environment on the production of form variants has resulted from the concept of phases in locusts. By linking together as mutually transformable through successive generations the previously supposed separate species of *Locusta migratoria* L., *L. danica* L., and *L. migratorioides* R. & F., Uvarov (1921) opened a fresh field of research in variation. In this paper the outline of the concept of phases is propounded, by which the new terms of " gregarious " and " solitary phases " become associated with the old specific names. The forms *migratoria* and *migratorioides*, with their generally dark colour and such biological characters as their gregariousness and migratory tendencies, were regarded as the gregarious phase, whilst the non-gregarious *danica*, with its typically green coloration and supposedly sedentary behaviour, was considered to be the solitary phase. Thus the implied contrast was between related aspects of morphology and behaviour.

The important point is, however, that these phases represent the extreme forms of variation in locusts. It now appears that this variation, which under the above theory involved both morphology and behaviour, is at least in part a response to the conditions of the environment. However, subsequent work has shown that these dual facets of morphology and behaviour need not simultaneously reflect a given state of the individual, so that a failure in this early period to formulate a more precise definition of phase has resulted in much confusion in later literature. The development of the Phase Theory and its present position has been excellently reviewed by Key (1950).

From the work of Faure (1923 and 1932), Plotnikov (1924) and others it soon became apparent that one of the major factors responsible for the production of the gregarious phase was the degree of crowding in the nymphal period, whilst isolation tended to produce the colour form of the solitary phase. At least from the morphological standpoint, similar responses to the condition of crowding have since been identified in various grasshopper forms such as those of the genus *Chorthippus* by Rubtzov (1935), *Melanoplus bivittatus* by

Grayson (1942), and in *Melanoplus mexicanus* Sauss. by Faure (1933) and Brett (1947). Thus much of the later work of Faure (1932), Volkonsky (1939), Ramchandra Rao (1942), Del Cañizo Gomez (1943), Andrewartha (1944), Haroon (1947) and others has been devoted to a study of the conditions which lead to population increases. Such increases, which also involve an associated increase in the degree of crowding, may lead to the formation of swarm outbreak centres by the gregarious phase locusts so produced.

The economic importance attached to an adequate control of the locust problem has given an impetus to the study of the occurrence of phase in the Acrididae, so that this type of response came to be regarded more as a special quality of locusts than as an extreme example of a more general biological principle. Poulton (1929) suggested that the Phase Theory might help to explain the periodic nature of butterfly migrations, but it was not till 1939 that a serious attempt was made by Klingstedt to widen the application of the theory to the animal kingdom in general, though, due to lack of evidence of this type of variation response beyond the Orthoptera, this must still remain hypothetical.

Poulton (1892) noted that the crowding of lepidopterous larvae tended to result in a darkening of their colour, and from time to time many entomologists who have bred caterpillars have noted that the captive specimens were darker than the naturally occurring wild form. However, if such darkening may be attributed to a condition of crowding, it would appear that such forms could be produced naturally in the field when the population density of the larvae was of the appropriate order. This has, in fact, turned out to be the case, so that Sneyd Taylor (1951) observed that a dark form he had not previously seen of the larva of the Sphingid *Chaerocampa celerio* L. was associated with an area in which they were especially numerous, whilst Lemche (1941 cited in manuscript) found almost black forms of the normally yellowish-white larvae of *Dasychira pudibunda* L. in heavily infested areas of Danish woodland.

Faure (1943), breeding the Southern Army Worms of South Africa, *Laphygma exigua* Hübn. and *L. exempta* Walk., showed, for the first time on an experimental basis, a darkening response in a non-Orthopteran form to a crowding condition. He further considered that the characteristics exhibited sufficiently typified those occurring in locusts to regard them as phasic. A degree of colour response was also obtained in the Noctuid *Spodoptera abyssinia* Guenée, but due to the fact that the behaviour was not noticeably affected, he did not consider this to be a phase variation parallel with that occurring in locusts, though Mathée (1947), on statistically analysing the form incidence in this species in relation to the breeding condition, obtained a significant result which he attributes to phase.

Sevastopulo (1943, 1944, 1945) carried out limited breeding experiments with certain Indian Sphingids, as a result of which he obtained a range of variations. Though many of his experiments were not confirmed, he attributed his results to a variety of causes, inferring amongst them that certain of the larvae were sensitive to crowding and may produce dark forms. In Great Britain the first systematic experiments involving a response to the larval population density were carried out by Williams and Long (1950) with the migrant moth *Plusia gamma* L., when a definite result was obtained by the production of dark forms in the crowded condition only.

From work not yet published it can now be shown that there are many aspects in the responses of lepidopterous larvae to crowding which may be parallel to those occurring in locusts. It may well be that the larval type of variation produced can be compared with the extremes produced in locusts, and that the principles involved are of the same general biological nature. It is certain that phase variants in locusts are not the response to one simple factor, but are the result of a complex reaction. Further, it can be expected that different complexes may produce similar end-effects. Thus with the grass-hopper *Melanoplus bivittatus* Grayson (1942) showed that nymphs reared at low temperatures produced an increase in their areas of black pigment over those reared at a high temperature, which resulted in a uniformly dark form. However, nymphs reared under crowded conditions also resulted in an increase in the amount of black pigment, whereas those reared in isolation resulted in the more generally dark form. Gregarious locusts are not only mutually excited but mutally attracted, and so give rise to coherent swarms. Lepidopterous larvae on the other hand, with the exception of the Army Worms, and possibly others, may show mutual excitement with an associated colour change, but there appears to be little evidence as yet in support of their exhibiting a truly gregarious behaviour pattern. It is apparent, therefore, that much further research must be done on the production of such variants if the true relationship between the form and its environmental condition is to be ascertained.

In this review, variation has been considered from the independent stand-points of the genetical and environmental bases and their possible interaction in producing the resulting variant. Phase variants, however, raise a new problem. In the case of locusts, the phase of the parents appears to influence the trend of the newly emerged hopper. Black hoppers are normally associated with gregarious parents, whilst the progeny of solitary parents are typically green. Further, Grayson (1942), referring to the non-swarming grasshoppers, considered that the colour type of the parent may condition the adult coloration of the F_1 generation. Although such phenomena may appear to support the idea of the inheritance of acquired characters, it must be remembered that the principle of the transmission of such factors is not known. At the same time, should the phenomena be shown to be of wide biological occurrence in producing variants, it must play a very important part in the life-histories of such forms in fitting them into their specific ecological niche.

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A NOTE ON THE VARIABILITY IN THE APPEARANCE OF THE BROOD IN SOME BRITISH LEPIDOPTERA.[1]

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INTRODUCTION.

IN 1946 studies were continued by the use of light-traps on the activity of certain species of nocturnal Lepidoptera in relation to weather conditions, as suggested by Williams (1940). This work was carried on for four years, and in 1949 a set of data was available comparable with that obtained by Williams between 1933 and 1936. This comparison was in every way valid as the type of trap and its position was in both cases identical, and the situation, on the border of one of the classical plots at Rothamsted Experimental Station, was particularly stable with respect to the surrounding vegetation and agriculture (Williams, 1939). These two sets of data for the 1933–36 and 1946–49 periods were therefore compared and then combined to give the information for the study of the variability in the appearance and length of the brood of seventeen species of nocturnal Lepidoptera for the eight years.

Each species used in this study was selected on the grounds of having a definite brood and on having captured over 300 individuals. The total number of individuals caught each year and the totals for each set of four years and for the eight years is shown in Table I, while the distribution of each species, i.e., the days on which these individuals were taken, is shown in fig. 1.

TABLE I.—*The number of individuals of each species in each year together with the totals for each 4 years and all 8 years.*

	1933.	1934.	1935.	1936.	Total for 1933–36.	1946.	1947.	1948.	1949.	Total for 1946–49.	Total for 1933–36 and 1946–49.
S. lubricipeda	179	126	83	79	467	140	94	102	114	450	917
S. lutea	100	73	40	34	247	48	27	52	84	211	458
R. umbratica	29	22	74	24	149	64	34	99	64	261	410
A. exclamationis	111	165	1799	381	2456	58	27	100	62	247	2,703
C. perlellus	208	476	564	287	1535	979	593	454	294	2320	3,855
A. monoglypha	30	90	603	20	743	21	22	54	15	112	855
L. impura	52	75	58	42	227	29	16	68	58	171	398
C. tristellus	815	1792	3979	633	7219	1236	539	641	1254	3670	10,889
E. lurideola	99	138	67	32	336	46	76	20	31	173	509
T. matura	38	33	75	53	199	67	27	24	16	134	333
N. ruralis	40	49	61	27	177	62	72	17	47	198	375
L. testacea	46	153	294	111	604	551	234	434	725	1944	2,548
A. xanthographa	210	100	172	105	587	168	61	89	217	535	1,122
A. c-nigrum (2nd brood)	57	81	300	106	544	497	658	919	2028	4102	4,646
T. popularis	39	109	132	30	310	71	52	45	58	226	536
O. lunosa	60	159	194	131	544	69	56	85	444	654	1,198
A. lychnidis	324	219	232	43	818	105	161	128	343	737	1,555
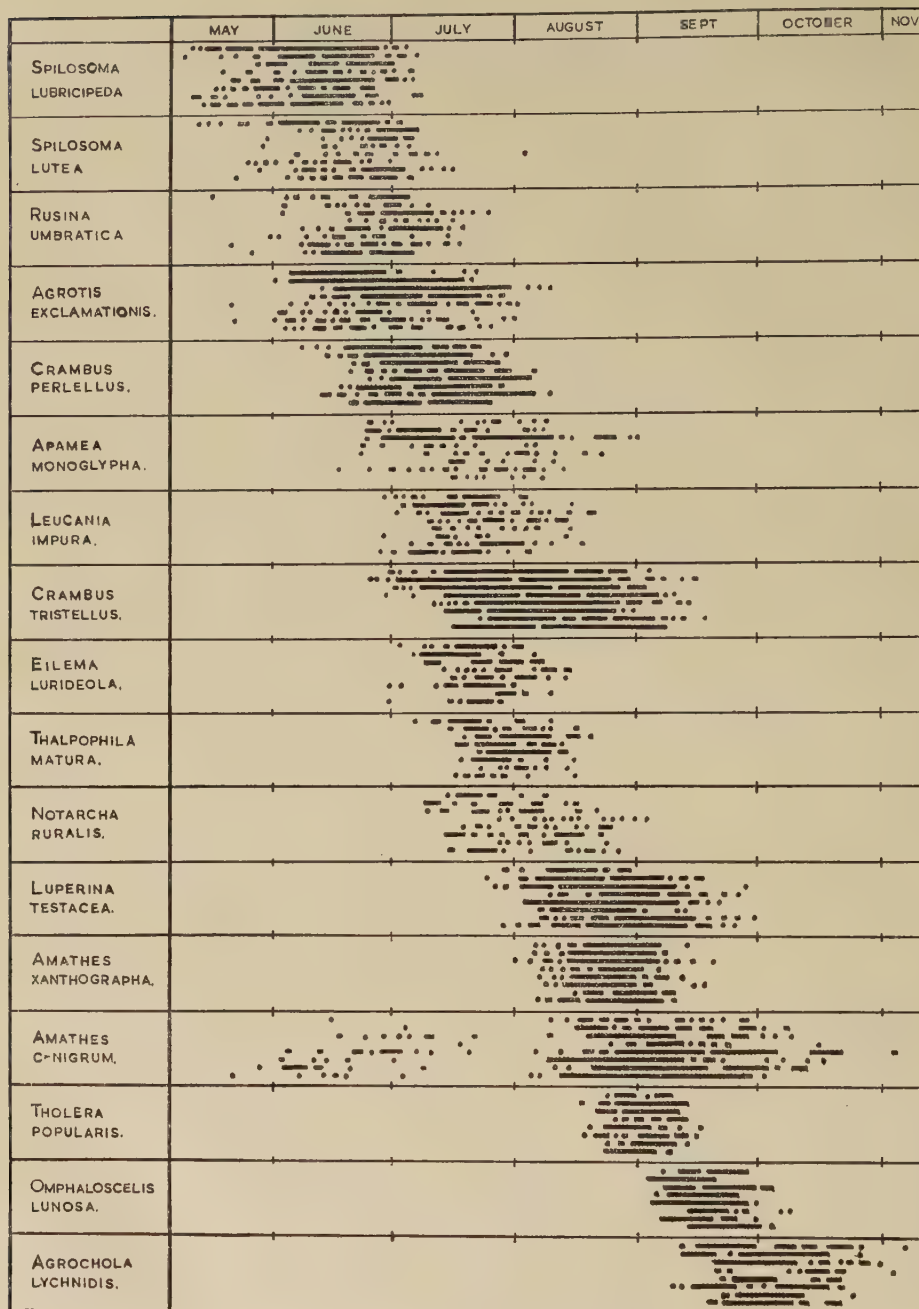
FIG. 1.—Dates of occurrence in each of the eight years 1933–36 and 1946–49 of seventeen species of Lepidoptera.

The nomenclature used in this paper is taken from *Indexed Check-List of the British Lepidoptera with the English Name of each of the 2313 Species*, by I.R.P. Heslop. 2nd edition, 1947.

THE VARIABILITY OF THE BROOD FROM YEAR TO YEAR.

To study the variability the brood was divided at five fixed points which were the dates when the first, 25 per cent., 50 per cent., 75 per cent., and the last individual of the brood was caught. Table II shows the mean date for these

TABLE II.—*Mean dates of certain fixed points during the brood of some species of Lepidoptera for 1933–36 and 1946–49.*

| | Mean date of appearance 1933–36 and 1946–49. | | | | | Mean length of brood in days. |
	First.	25%.	50%.	75%.	Last.	
S. lubricipeda .	16 May	6 June	13 June	19 June	7 July	52
S. lutea . .	28 ,,	15·5 ,,	21 ,,	27·5 ,,	11 ,,	44
R. umbratica .	1 June	19 ,,	27 ,,	3 July	14 ,,	43
A. exclamationis .	2·5 ,,	19 ,,	26·5 ,,	4·5 ,,	28 ,,	55·5
C. perellus .	17·5 ,,	1·5 July	8 July	15 ,,	1·5 Aug.	45
A. monoglypha .	27 ,,	8·5 ,,	18·5 ,,	26 ,,	14·5 ,,	48·5
L. impura . .	3·5 July	15 ,,	21 ,,	28 ,,	12 ,,	39·5
C. tristellus .	7·5 ,,	31 ,,	6·5 Aug.	14 Aug.	9 Sept.	63·5
E. lurideola .	9·5 ,,	19·5 ,,	24·5 July	28 July	6·5 Aug.	28
T. matura . .	17 ,,	24 ,,	28·5 ,,	3 Aug.	15 ,,	29
N. ruralis . .	17·5 ,,	25·5 ,,	1 Aug.	8·5 ,,	22·5 ,,	36
L. testacea . .	2 Aug.	15 Aug.	24 ,,	31 ,,	18 Sept.	47
A. xanthographa .	7·5 ,,	20·5 ,,	24·5 ,,	29 ,,	12 ,,	35·5
A. c-nigrum . (2nd brood)	11·5 ,,	29·5 ,,	6 Sept.	12 Sept.	12·5 Oct.	62
T. popularis .	21·5 ,,	29 ,,	2 ,,	5·5 ,,	12 Sept.	21·5
O. lunosa . .	7 Sept.	14 Sept.	17 ,,	20·5 ,,	30 ,,	23
A. lychnidis .	16 ,,	26·5 ,,	2·5 Oct.	7 Oct.	25·5 Oct.	39·5

Mean length of brood 42
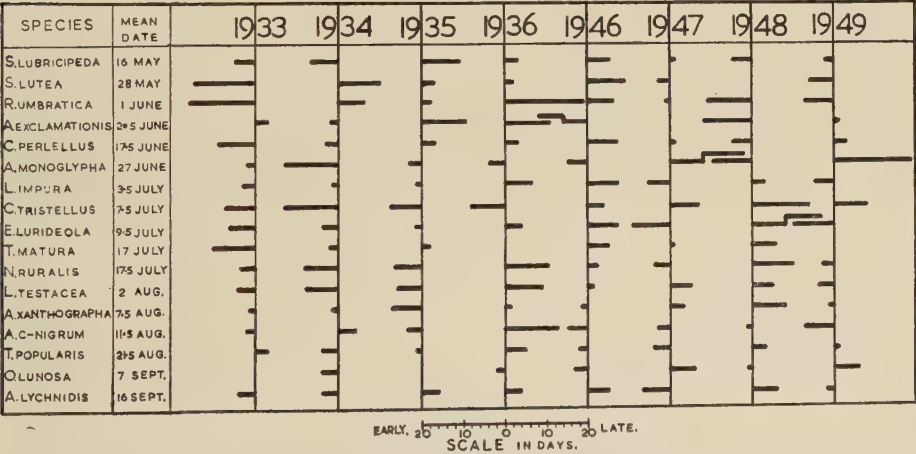
FIG. 2.—Mean dates of first appearance and departures from the mean in each year of some species of Lepidoptera.

five fixed points for each species selected, together with the mean length of the brood in days.

In fig. 2 the departures of each species from the eight-year mean for the first appearance is shown, and similar diagrams can be constructed at each of the other four levels of the brood.

From Table II and the actual dates of appearance the difference from these means can be obtained, and by summing the squares of these differences for each year a measure of the variability is available. These sums of squares (the variability) of each species at each level are shown in Table III, together with the mean sum of squares at each level, the standard deviation and error of the mean. The mean variability for each species is given in the last column.

TABLE III.—*Variability of certain fixed points during the brood of some species of Lepidoptera for 1933–36 and 1946–49.*

	First.	25%.	50%.	75%.	Last.	Mean.
S. lubricipeda	219	**363**	282	*159*	297	264
S. lutea	464	341	*192*	234	**824**	411
R. umbratica	**864**	179	162	*140*	328	335
A. exclamationis	**520**	412	*273*	371	339	383
C. perellus	204	*163*	179	283	**286**	223
A. monoglypha	**1008**	391	371	*336*	519	525
L. impura	*170*	194	211	**297**	293	233
C. tristellus	**694**	385	513	408	*301*	460
E. lurideola	**604**	314	*175*	357	300	350
T. matura	170	148	**200**	155	*61*	147
N. ruralis	376	**662**	565	459	*386*	490
L. testacea	264	*190*	221	276	**657**	322
A. xanthographa	126	76	51	*28*	**161**	88
A. c-nigrum (2nd brood)	290	*202*	457	540	**892**	476
T. popularis	**70**	*24*	39	52	45	46
O. lunosa	102	103	104	*83*	**227**	124
A. lychnidis	178	*101*	171	203	**407**	212
Mean sum of squares	371·9	249·9	245·1	257·7	371·9	299·4
Standard deviation	7·3	6·0	5·9	6·1	7·3	6·5
Error of means	2·6	2·1	2·1	2·1	2·6	2·3

As can be seen from Table III, the highest variability occurs in the first and last appearance of the brood; in actual fact these two points have exactly the same mean variability. The lowest variability occurs at the 50 per cent. level, with the 75 per cent. level being slightly more variable than the 25 per cent. level but the error of the mean differs by only half a day at all five levels. It would therefore appear that the variability of the date is less during the course of the brood than at the first or last date, i.e., there is a tendency to compensate for any earliness or lateness in first appearance by the speeding up or retarding of emergence during the brood. In Table III the highest variance for each species is in heavy type and the lowest in italics. It will be seen that the first appearance has six maxima and two minima, the 25 per cent. level two and five, the 50 per cent. level one and three, the 75 per cent. level one and five, and the last appearance seven maxima and two minima. Thirteen of the seventeen species have their maxima in the first or last group, and thirteen of the minima lie in the 25, 50 and 75 per cent. groups.

DISTRIBUTION OF THE BROOD.

The mean length of the brood as shown in Table II is forty-two days, and the peak of the distribution might be expected to occur at or near the middle of the duration of the brood, with the brood as a whole symmetrically distributed about this point. The actual shape of the distribution was studied by the use of Table IV, in which the number of days taken for each species to reach the various points

TABLE IV.—*Mean number of days taken by some species of Lepidoptera at different levels from the date of first appearance for 1933–36 and 1946–49.*

	First.	25%.	50%.	75%.	Last.
S. lubricipeda . .	16 May	21	28	34	52
S. lutea . .	28 ,,	18·5	24	30·5	44
R. umbratica . .	1 June	18	26	32	43
A. exclamationis .	2·5 ,,	16·5	24	33	55·5
C. perlellus . .	17·5 ,,	14	20·5	27·5	45
A. monglypha . .	27 ,,	11·5	21·5	29	48·5
L. impura . .	3·5 July	11·5	17·5	24·5	39·5
C. tristellus . .	7·5 ,,	23·5	30	37·5	63·5
E. lurideola . .	9·5 ,,	10	15	18·5	28
T. matura . .	17 ,,	7	11·5	17	29
N. ruralis . .	17·5 ,,	8	14·5	22	36
L. testacea . .	2 Aug.	13	22	29	47
A. xanthographa .	7·5 ,,	13	17	21·5	35·5
A. c-nigrum . . (2nd brood)	11·5 ,,	18	25·5	31·5	62
T. popularis . .	21·5 ,,	7·5	11·5	15	21·5
O. lunosa . . .	7 Sept.	7	10	13·5	23
A. lychnidis . .	16 ,,	10·5	16·5	21	39·5
Average . . .	0	13·44	19·71	25·71	41·91
Interval . . .		13·44	6·27	6·00	16·20

in the duration of the brood was listed. The average for each level was found, and the intervals between them taken and plotted as shown in fig. 3. Upon this
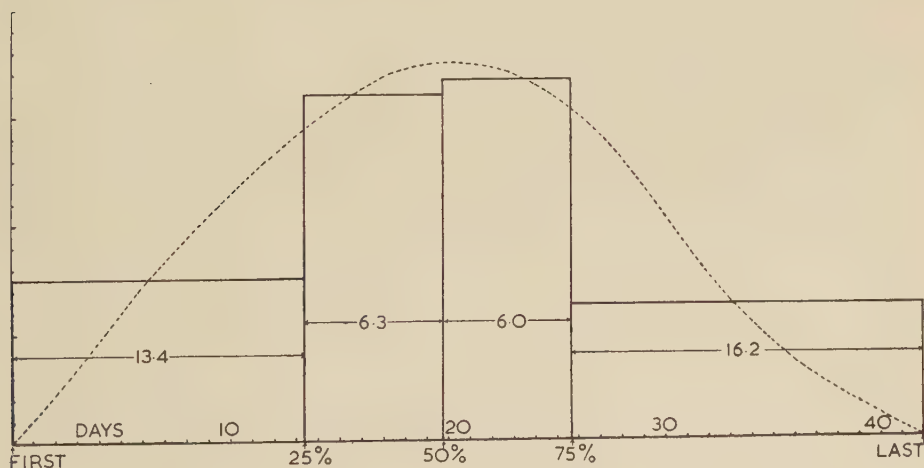
FIG. 3.—The average number of days taken to reach the different percentages of the total brood.

histogram a curve was superimposed, and from this it can be seen that the distribution of the brood is slightly asymmetrical, with a tendency to prolong the duration of the last quarter of the brood.

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A PRELIMINARY INVESTIGATION INTO THE LOCOMOTION OF AQUATIC HEMIPTERA AND COLEOPTERA.

By E. J. Popham, D.Sc., Ph.D., F.R.E.S.

It is generally agreed that the Insects are a group of animals which have evolved from terrestrial Arthropoda and are, therefore, primarily adapted for terrestrial life. Amongst the Hemiptera and Coleoptera there are a number of families in which the species are adapted for life in fresh water. In a series of papers (1947*a*, *b*, *c* and 1949) Thorpe and Crisp have recently described the plastron respiration of various species belonging to the families Elmidae and Dryopidae among the Coleoptera and of the Hemipteron, *Aphelocheirus aestivalis* Westwood. All of these are small insects which are heavier than water. In contrast to these interesting insects we find species belonging to these two orders in which the insects have a specific gravity greater than that of water, but they carry large reserves of air upon the body surface which makes them lighter than water. Examples are to be found in the Corixidae, Notonectidae, Naucoridae and Dytiscidae.

The presence of these reserves of air causes the insects to float upwards towards the surface. While swimming they have, therefore, three forces acting on them, namely, (1) the buoyancy of the air stores, (2) the resistance of the water, and (3) the motion given to the insects by the legs.

The buoyancy may be regarded as having a more or less constant value from one stroke to the next, but it decreases as the insects descend to greater depths of water. Observations on the Notonectidae and Corixidae have also shown that there is a conspicuous loss of buoyancy with continued submergence at temperatures over 15° C. This seems to indicate that, although the reserves of air may act as a physical gill (Ege, 1915), yet at higher temperatures, where the solubility of the oxygen is reduced, the increased metabolic rate of the insects requires a greater supply of oxygen than that which can be obtained by diffusion into the air bubbles.

For practical reasons the resistance of the water must be assumed to be proportional to the swimming speeds, but as these are of the order of only a few centimetres per second, this assumption is probably justified.

In the Corixidae and Notonectidae, as well as in the Dytiscidae, the hind legs are flattened and edged with hairs and are used as organs of locomotion. These are the only legs used for locomotion in many of the species of these families ; the greatest speeds are attained during the leg kicks and while the legs are being returned to their original position the resistance of the water retards the insect and may, in the case of *Notonecta*, actually bring it to a standstill. Because the insect is being raised by the buoyancy of the air stores, it can only progress along a horizontal path some distance below the surface if the kicks are of such a nature as to propel the insect downwards. If the action of the legs is assumed to be instantaneous (which at higher temperatures is a not unreasonable assumption), the motion of the insect may be compared to that of an inverted projectile.

In fig. 1 the point o represents the position of the insect at the start of the leg kick. The line opq is the path taken by the insect, here represented by the letter P. The tangent to the curve opq at the point o makes an angle α with the line ox and indicates the initial path of the insect. If the next leg kick takes place when the point P reaches the axis ox, the insect will progress forwards

along a horizontal path, as shown in fig. 2. If, on the one hand, the rate of leg beat is accelerated so that the second leg kick begins before P has crossed the ox axis, then the insect will swim deeper into the water. On the other hand, if the rate of leg beat is retarded so that the next leg kick begins after P
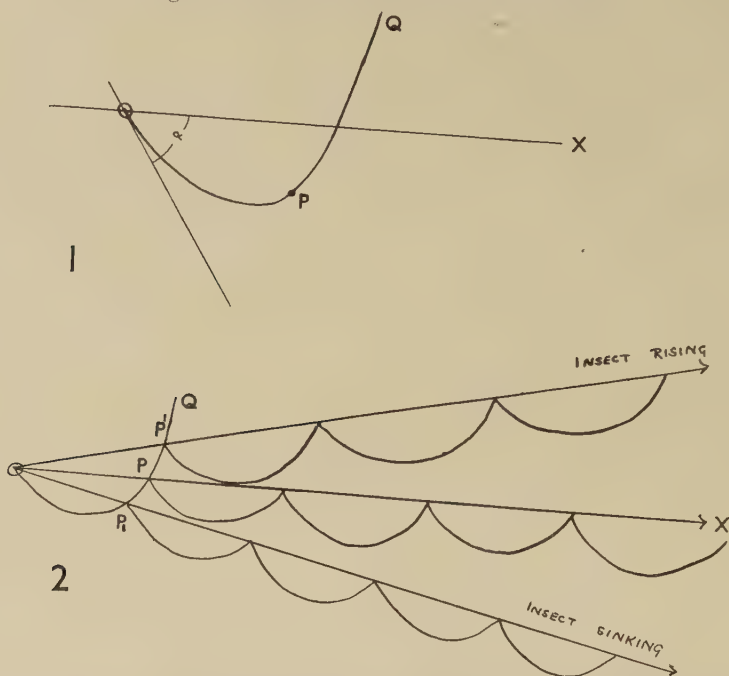
FIGS. 1, 2.—When the rate of leg beat is accelerated the insect swims deeper into the water, rising again when the leg beat is retarded. For details and explanation of lettering see text, p. 117.
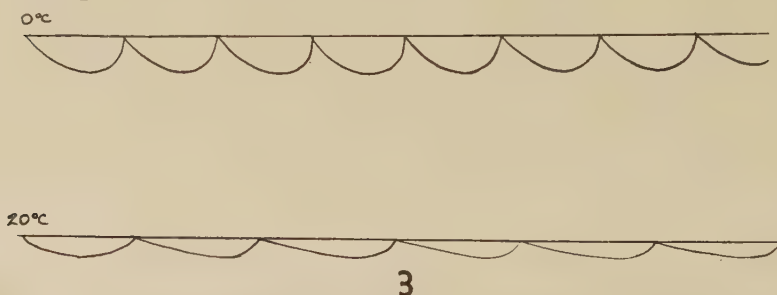
FIG. 3.—At 0° C. angle α is larger than at 20° C. It will also be observed that, although the rate of leg beat is greater at 20° C., the legs are more efficient and so fewer leg beats are required at 20° C. to carry the insects over a given distance.

has crossed the ox axis, then the insect will rise into shallower water. These two phenomena can in fact easily be observed when the insects swim to and from the surface of the water.

The value of angle α varies from one species to another, and even within the same species. For example, in *Notonecta* the insect starts with the dorsal surface of the body forming an angle of about 30 degrees with the surface of the water. As the hind legs are moved backwards the inclination is increased

to 55 degrees and it is driven downwards at that angle. Progress from one point to another would be slow were the insect not able to turn over and swim in a normal dorso-ventral position in which there is less surface resistance, so that the variations in the level of the insect during each stroke are greatly reduced. As the temperature is raised, the rate of leg beat increases and the legs also become more efficient as organs of locomotion. This is associated with a decrease in the value of angle α, in order to keep the insect travelling in the same direction (fig. 3). The action of the legs varies with the temperature. For example, at 2° C. the legs of Corixids are moved comparatively slowly in a horizontal plane through an angle of about 120 degrees. The stroke begins in a position where the legs are pointing forwards, and ends in one in which the tips of the tarsi touch each other just behind the posterior end of the abdomen; the speed at which they are moved reaches a maximum when at right angles to the body. At higher temperatures the legs are moved through proportionately smaller angles so that at 25° C. this may be only 30 or 40 degrees. As the temperature is raised the legs become more efficient and the general locomotion of the body more uniform.

The rate of leg beat seems to be determined by impulses from the cerebral ganglia as well as the thoracic ganglia. If a Corixid is decapitated a regular leg beat is developed after an interval of 5 to 10 minutes, but at a slower rate than normal. This leg movement, which is the result of impulses from the thoracic ganglia, has little or no ventral component, so that the insect swims horizontally at the surface or forwards in whatever position it happens to be placed. It would appear that this basic leg movement may be accelerated by impulses from the cerebral ganglia, which also control the orientation of the insect itself to various stimuli. A sudden change of about 15° C. in the temperature of the head invariably brings the insect to the surface and produces a mode of behaviour not unlike that of a decapitated insect.

The large Water Beetle, *Dytiscus marginalis* L., does not progress through the water in a jerky manner. At 0° C. the hind legs beat quite slowly, yet the speed of the insect remains comparatively uniform. The reason is that in this species the pro- and meso-thoracic legs are flattened and to some extent take part in locomotion, but, as their movement alternates with that of the hind legs, the insect continues to move at a more or less constant speed.

The locomotion of these Hemiptera and Coleoptera is being investigated and it is hoped to publish a more detailed account at a later date.

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